MONOGRAPH OF THE GENUS *SPIALIA* SWINHOE (LEPIDOPTERA, HESPERIIDAE)

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With seven plates and 119 text-figures

ABSTRACT

The genus *Spialia* Swinhoe is distributed throughout the Afrotropical Region and in large parts of the Palaearctic and Oriental Regions. Of the 26 species, 18 are confined to the Afrotropical Region. The species are classified into seven species groups, which are mainly based on characters of the male and female genitalia. Two subspecies are described as new, viz., *Spialia colotes semiconfluens* and *Spialia depauperata australis*. A key to the species based on external characters is provided and drawings of the male and female genitalia, photographs of the skippers and distribution maps of the species are given.

A number of characters is analysed as to their plesiomorphous or apomorphous conditions, resulting in an outline of the evolutionary history and providing the phylogenetic arguments for the classification adopted. Combined with known ecological changes in the past, this outline affords a means for the reconstruction of the geographic history.

The genus is generally at home in dry open country. One species is restricted to the African forests; it is shown that this habitat preference is apomorphous with respect to the preference for open country. Due to the latter preference the development of the genus in Africa has been greatly influenced by the alternation of dry and wet periods in the past causing changes in the extent and continuity of the savanna area. Most, if not all, species existing at present originated during the Pleistocene. At various times and to various degrees *Spialia* species succeeded in invading areas outside the Afrotropics, giving rise to secondary radiation. Successful establishment in the Palaearctic was accompanied by a change to other food plants. Only one, apparently recent, re-invasion into Africa can be recognized, viz., by *S. doris*, a semi-desert species.

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1. INTRODUCTION

General

The genus *Spialia* has not yet been studied as a whole. This is probably due to the fact that its members are distributed over three zoogeographic regions, viz. the

Palaearctic, Oriental and Afrotropical Regions. So we have reviews of the Palaearctic species (e.g., Warren, 1926; Picard, 1947) and of the Afrotropical species (Higgins, 1924; Evans, 1937). Especially the last ones are interesting as the bulk of the species occurs in the Afrotropical Region. The last review, however, of the Afrotropical species is 40 years old. Apart from the fact that new information has become available, the female genitalia have never been described, so it does not seem superfluous to give a revision of the whole genus.

Preliminary to this paper I published a paper on the Palaearctic *Spialia* species (De Jong, 1974). As the variation and distribution of the Palaearctic species are far better known and their evolutionary and geographic history can far better be traced back than those of the Afrotropical species, a separate treatment seemed appropriate. For the sake of completeness, however, the Palaearctic species will also be dealt with in the present paper, although for details the reader is referred to my earlier paper on *Spialia*. I may also refer to that paper for notes on the distinction of subspecies and for methods and measurements.

The study of this genus is facilitated by the fact that many types are located in a single collection: the types of 37 of the 59 names applying to species and subspecies (including synonyms) are in the collection of the British Museum (Nat. Hist.), apart from a number of types of seasonal and individual varieties.

It is attempted to give a classification that reflects the phylogenetic relationships. In Chapter 4 the evolutionary history that forms the basis for the classification is dealt with. It is unfortunate that many parts of Africa have still been badly explored as to the Hesperiidae, thus making the study of the zoogeography of the genus difficult. Moreover, literature records on the distribution cannot always be relied on, as I found many misidentifications in the collections, even by Evans. This is undoubtedly partly due to the fact that good drawings of the genitalia do not exist, the drawings by Evans only giving a vague idea that they represent genitalia. Therefore, drawings of the male and female genitalia of all species are presented in the present paper. Photographs have been added of the upper and underside of all species, as I think a good photograph is more instructive than a page-long description. In this way I hope this paper will be a stimulus to fill the many gaps in our knowledge.

Delimitation of the genus *Spialia*

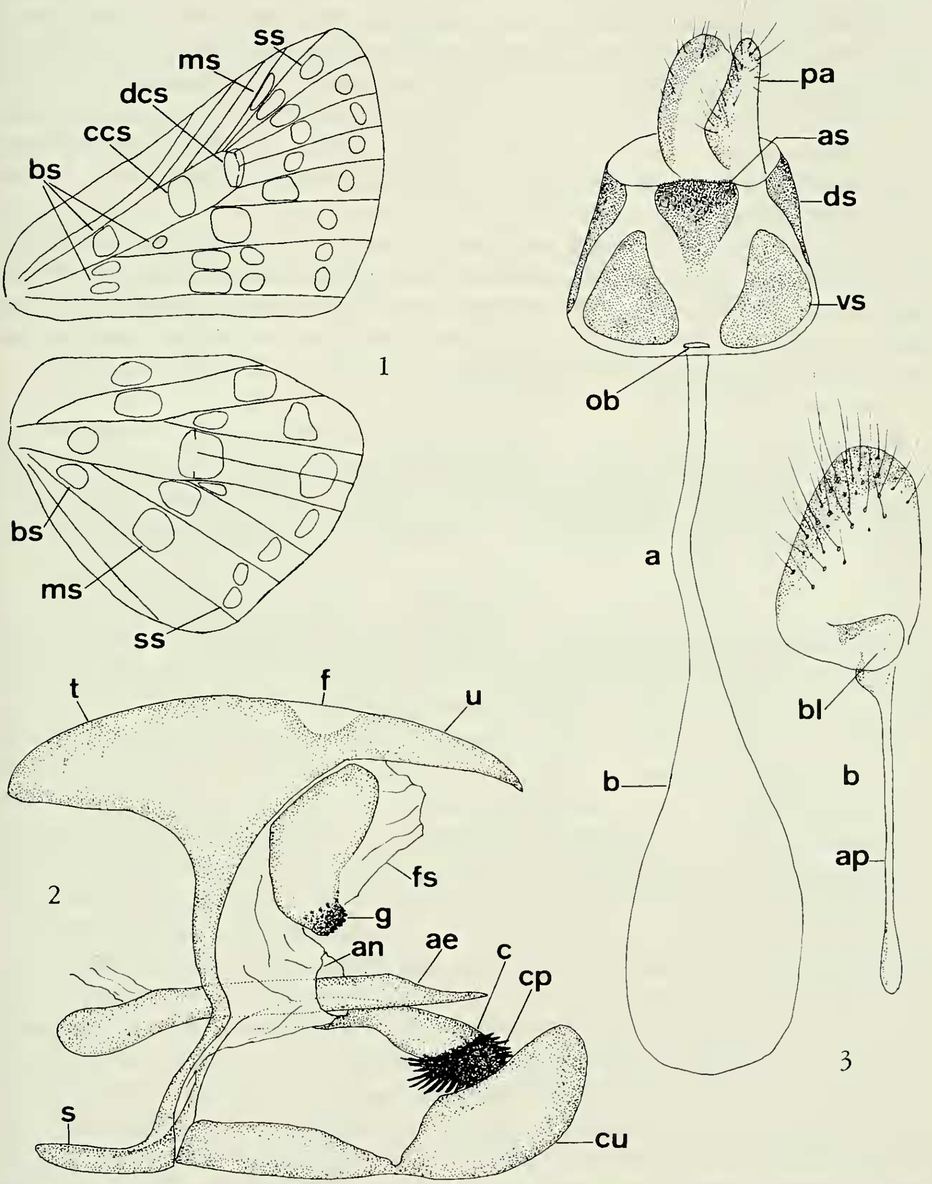
The genus *Spialia* Swinhoe, 1913 (type species *Hesperia galba* Fabricius, 1793, by original designation) comprises those black-and-white skippers that have the median spots in spaces 4 and 5 of the fore wing upperside (if present) in line with those in spaces 6 to 8, the median spot in space 2 of the fore wing upperside central between the central cell spot and the median spot in space 3 or nearer the latter, the termen of the hind wing evenly rounded without crenulation, no tibial hair tuft on the hind legs in the male and usually no costal fold in the male.

For more information on the differences and relationship with other genera, I may refer to a forthcoming paper on the generic classification of the *Pyrgus* group.

Wing markings

The wing markings of *Spialia* species are essentially the same as those of

Pyrgus species (see De Jong, 1972). In principle, each internervular space has three spots, viz., a basal, median and submarginal spot. In addition, there is a basal



Figs. 1—3. Wing markings, male and female genitalia of *Spialia*. 1. Wing markings. bs, basal spots; ccs, central cell spot; dcs, discoidal spot; ms, median spots; ss, submarginal spots. 2. Male genitalia, lateral aspect (left valva removed). ae, aedeagus; an, anellus; c, costa; cp, costal process; cu, cucullus; f, fenestrula; fs, fultura superior; g, gnathos; s, saccus; t, tegumen; u, uncus. 3. Female genitalia; a, ventral aspect; b, papilla analis. ap, apophysis posterior; as, area spinulosa; b, bursa; bl, basal lobe; ds, dorsal sclerite of eighth abdominal segment; ob, ostium bursae; pa, papilla analis; vs, ventral sclerite of eighth abdominal segment.

cell spot, a central cell spot and a discocellular spot covering the discocellular veins. The markings may be very reduced, all basal spots may be absent and there are no submarginal spots in spaces 8 to 12. In space 1b of the fore wing the spots can often be seen divided into an upper and lower part, indicating the lost second cubital vein (if we consider veins 2 and 3 branches of the first cubital vein). Moreover, in this space the median spot is double, being divided into an inner and outer spot, which in their turn may be divided into an upper and lower part. So there may be four median spots in space 1b of the fore wing, the relative development of which is important in the distinction of some species. In *Spialia* one of these spots is always absent.

The markings of the hind wing are simplified as compared with those of the fore wing. The median spots on the underside of the hind wing are usually fused together and to the discocellular spot to form a more or less regular band (the median band) parallel to the termen. In a few species these spots are separate and in a few others the band is not parallel to the termen.

A diagram of the usual spots in *Spialia* is presented in fig. 1.

As the expression "median spot in space x" is unnecessarily long, it is abbreviated in this paper to "median spot x". The median spots in space 1b of the fore wing will be distinguished as the inner and outer median spots 1b and 1c, the latter designing the upper part. Median spot 1a (between vein 1 and dorsum) is always absent.

Genitalia

Male (fig. 2). Although relatively simply built, the male genitalia offer a good means for the identification of most species and much of the relationships between the species becomes clear when studying the male genitalia.

The uncus is rather short and entire, except in four species where it is bifid. The apex of the uncus is pointed or inflated. The junction of the uncus with the tegumen is often well visible as a narrow, more or less membranous suture and in some species this suture is broadened mid-dorsally to a triangular or quadrangular membranous area, called fenestrula (cf. Ogata et al., 1957). The gnathos is a simple sclerotized fold or, usually, has various spined structures in the ventral part; dorsally it is free or fused with the tegumen over some distance. The fultura superior is smooth or finely spined and often passes imperceptibly into the central part of the gnathos. The anellus is membranous or dorsally sclerotized and may bear strong spines. The aedeagus is variously built, with a smooth surface or with spines, crests, side-arms, etc., often characteristic of a species group.

The valvae have usually a little developed cucullus, that often forms a fold to envelop partly the costal process. In some species the cucullus is spined. The most strongly differentiated part of the valvae is the distal part of the costa that often forms a process with spines or long hairs and is important for the distinction of species and species groups.

Female (fig. 3). The eighth abdominal segment usually bears two dorsal sclerites, but in a few species there is only a single sclerite. In most species the dorsal sclerotization is free from the ventral sclerites. In principle, the ventral sclerotization consists of two plates mid-ventrally separated by a membranous region which is narrow near the ostium, but broadens caudally. This membranous area is often slightly sclerotized and finely spinose in a more or less triangular patch. The spines are especially visible along the caudal rim of the segment, where the membrane folds inward. The slightly sclerotized spined area is called "area spinulosa" here. In a number of species the area spinulosa is solidly sclerotized and fused with the ventral sclerites to a single ventral sclerite. If strongly sclerotized, the area spinulosa may lack the spines.

The ostium is situated close to the anterior edge of the eighth segment. The narrow antevaginal region is usually membranous, but the ventral sclerites may be fused here. The ductus bursae varies in length and is entirely membranous except for some sclerotization near the ostium in some species. Usually it passes gradually into the bursa copulatrix, which is without ornamentation, except in one species in which the bursa bears a field of fine spines. The papillae anales are variously shaped, in a number of species with a fold that partly or entirely covers the base of the apophyses posteriores; this fold is called the "basal lobe" here.

Distribution

It is obvious that the distribution of the *Spialia* species is only imperfectly known. Nevertheless, I am convinced that the distribution maps roughly indicate the ranges of the species and additional material will mainly fill in the details (especially in West Africa), rather than extending the known ranges.

Under the heading "Localities" in the treatment of the species the countries in the Afrotropical Region have been arranged from Sudan and Saudi-Arabia southward through East Africa to South Africa and from there northward through Central and Westcentral Africa to Senegal. The localities in each country have been listed alphabetically.

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2. KEY TO THE SPECIES AND CHECKLIST

The distinction of species groups proposed in this paper is based on the male and female genitalia. These groups can be recognized only incompletely by external characters. As it is quite well possible to identify the species by their external characters, it seems best not to bother with species groups in the key, otherwise the characters of the genitalia should be introduced in the key, diminishing its practical value (viz., identification of species). To facilitate reference to the descriptions in Chapter 3, the species group to which a species belongs, is mentioned in the key. In cases of uncertain identification the genitalia should always be referred to.

1. On fore wing upperside, central cell spot closer to discocellular spot than to basal cell spot, basal spots in spaces 9 and 10 usually well developed (lying over the central cell spot) (fig. 4); male with costal fold 2

— On fore wing upperside, central cell spot not closer to discocellular spot than to basal cell spot, or basal cell spot absent; no spots in spaces 9 and 10 4

2. Basal spot 7 on hind wing underside fused to median band along vein 7, so that basal spots 7 and 8 together with the median band form a Y; on fore wing upperside submarginal spots incomplete, often only 4 and 5 present (*asterodia* group) . . . . *kituina*

— Basal spot 7 on hind wing underside not fused to median band; on fore wing upperside submarginal spots well-developed 3

3. Median band on hind wing underside with irregular edges, parallel to the series of basal spots; fringes not conspicuously spotted on underside (*asterodia* group) . . . . *asterodia*

— Median band on hind wing underside very irregular, along vein 2 pointing basad and reaching series of basal spots; fringes conspicuously chequered black and white on underside (*asterodia* group) . . . . *agylla*

4. Submarginal spots 4 and 5 of hind wing not in line with other submarginal spots, being placed more basad (fig. 10); male with costal fold 5

— Submarginal spots 4 and 5 of hind wing in line with other submarginal spots; male without costal fold 6

5. Median band on hind wing upperside composed of separate spots (*colotes* group) .... *colotes*

— Median spots on hind wing upperside fused into a continuous band (*colotes* group) .... *confusa*

6. Median spot 6 on hind wing underside absent or very small, not connecting the large central spot to one of the spots in space 7 (figs. 11—13) 7

— Median spot 6 on hind wing underside present, connecting the central spot (in spaces 4—5) with one of the spots in space 7 (figs. 14—15) 13

7. Median band on hind wing underside directed towards inner spot in space 7 (fig. 11); fore wing upperside without basal cell spot; Palaearctic species 8

— Median band on hind wing underside directed towards outer spot in space 7, or towards a point central between the inner and outer spots in space 7 (fig. 12); fore wing upperside usually with basal cell spot, but this spot sometimes vaguely outlined; Palaearctic and Afrotropical species 9

8. Ground colour of hind wing underside red in various shades, from ochreous to a very vivid red; central spot of hind wing underside angular; Europe and North Africa (*sertorius* group) .... *sertorius*

— Ground colour of hind wing underside greenish or yellowish olive-grey (except in the Asian ssp. *carnea,* where it is red); central spot of hind wing underside rounded; E. Europe to E. Asia (*sertorius* group) .... *orbifer*

9. On hind wing underside, inner spot in space 7 central between basal cell spot and median spot 4—5 (= central spot); median band directed towards a point between inner and outer spots in space 7; Palaearctic species (*phlomidis* group) .... *osthelderi* and *geron*

— On hind wing underside, inner spot in space 7 closer to basal cell spot than to central spot; median band directed towards outer spot in space 7; Palaearctic and Afrotropical species 10

10. On hind wing underside basal spot 1c absent, median spot 6 present, but small; on fore wing upperside discocellular spot strongly curved and outer median spot 1b usually present; a subdesert species (*phlomidis* group) *doris*

— On hind wing underside basal spot 1c present, median spot 6 absent; on fore wing upperside discocellular spot usually less strongly curved or straight, outer median spot 1b usually absent 11

11. On hind wing underside median spots 1c—5, basal cell spot and basal spot 1c shining white, median spots 1c and 2 entirely fused, no spot between median and submarginal spots in space 1c (*dromus* group) .... *paula*

— All spots on hind wing underside plain white 12

12. No light spot at base of costa on fore wing upperside; hind wing underside without a spot between median and submarginal spots in space 1c, inner spot in space 7 usually narrow and irregular, submarginal spot 1c double, the upper part out of line, median spot 1c usually not joined to median spot 2 (*sertorius* group) .... *mafa*

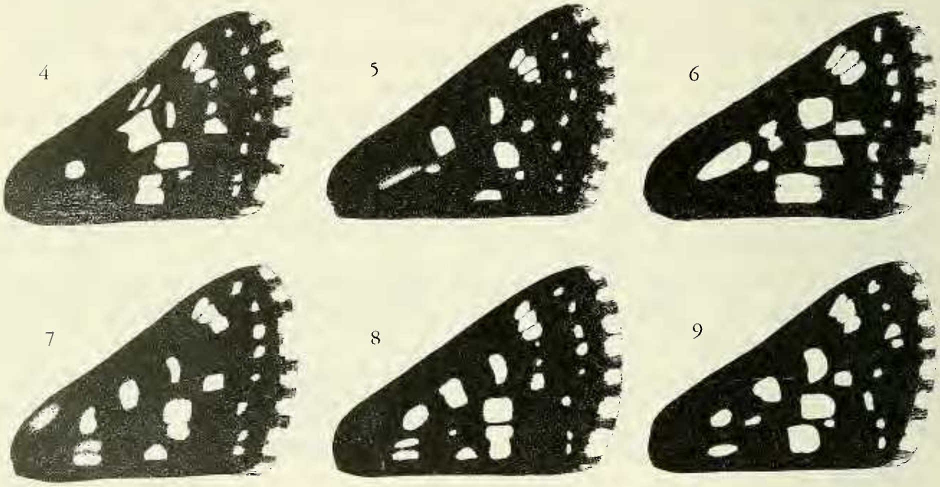
— Usually a light spot at base of costa on fore wing upperside (fig. 7); hind wing underside with a spot between median and submarginal spots in space 1c, inner spot in space 7 usually large and rounded, submarginal spot 1c usually single, median spot 1c joined to median spot 2 (*spio* group) .... *spio*

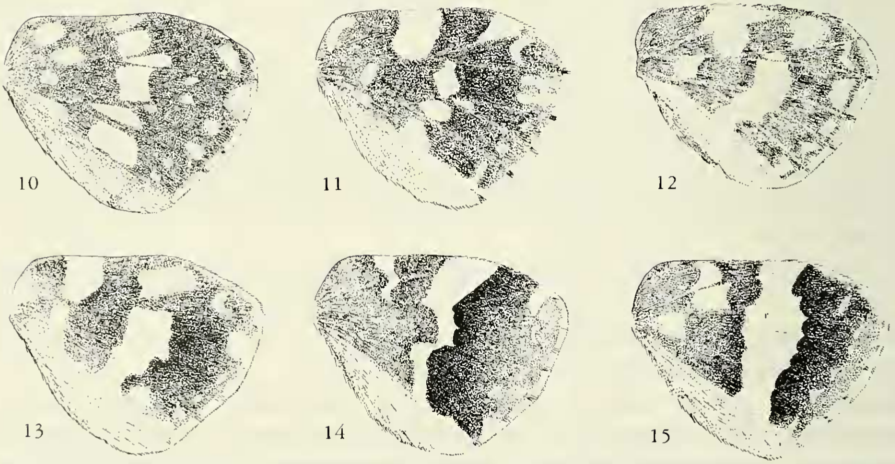
13. Median spot 6 on hind wing underside joins central spot to inner spot in space 7; Palaearctic species (*phlomidis* group) .... *phlomidis*

— Median spot 6 on hind wing underside joins central spot to outer spot in space 7; Afrotropical and Oriental species 14

14. Fore wing upperside without basal cell spot, at most some white scales forming a small dash against cubitus (fig. 5) 15

— Basal cell spot on fore wing upperside present (figs. 6, 8, 9) 20





Figs. 4—9. Upperside of right fore wing of *Spialia* species. 4, *S. asterodia*. 5, *S. zebra*. 6, *S. wrefordi*. 7, *S. spio*. 8, *S. diomus*. 9, *S. dromus*.
Figs. 10—15. Underside of left hind wing of *Spialia* species. 10, *S. colotes*. 11, *S. sertorius*. 12, *S. osthelderi*. 13, *S. spio*. 14, *S. nanus*. 15, *S. secessus*.

15. Submarginal spots entirely absent on upper and underside of fore and hind wings; hind wing underside without basal spots or a very vague one in space 7 (*delagoae* group) .... *mangana*
— On upper and underside submarginal spots at least partly visible 16
16. Hind wing underside without basal cell spot; median spot 6 on hind wing upperside absent or at most vaguely indicated 17
— Hind wing underside with basal cell spot; median spot 6 on hind wing upperside present or absent 18
17. Median band on hind wing underside winding (fig. 14) (*delagoae* group) .... *nanus*
— Median band on hind wing underside straight (*delagoae* group) . . *delagoae*
18. Submarginal spots on hind wing underside absent or very vaguely indicated along inner edge of light region along termen; median band slightly winding (*delagoae* group) .... *sataspes*
— Submarginal spots on hind wing underside present; median band straight 19
19. On hind wing upperside median spots reduced, usually only 2 and 4—5 visible; length of fore wing usually less than 11 mm (*delagoae* group) .... *zebra*
— On hind wing upperside usually median spots 2—6 present in a more or less straight band that is crossed by veins 3, 4 and 6; length of fore wing usually more than 11 mm (*delagoae* group) .... *depauperata*
20. On fore wing upperside, outer median spots 1b and 1c forming a bar from vein 1 to vein 2; inner median spot 1c absent and 1b usually smaller than one of the outer median spots (fig. 8); mid-tibiae spined (*spio* group) ...... *diomus*
— On fore wing upperside, outer median spot 1b absent; inner median spot 1b as large as or larger than outer median spot 1c, which may be absent; mid-tibiae without spines, except for the apical pair (as in all other species of the genus) 21
21. Median band on hind wing underside ends on termen 22
— Median band on hind wing underside ends on dorsum 23
22. Hind wing underside with a white streak from top of median band (median spot 7) to end of vein 5 at termen, veins lighter than ground colour; on hind wing upperside median band not divided by dark veins; on fore wing upperside submarginal spots complete, forming a sinuous series (angled at vein 5) (*dromus* group) .... *ploetzi ploetzi*
— White streak from top of median band to end of vein 5 on hind wing underside absent or scarcely visible and veins not lighter than ground colour; on hind wing upperside median band divided by dark veins; submarginal spots on fore wing upperside less conspicuous, not always complete, and series less sinuous (*dromus* group) .... *ploetzi occidentalis*
23. Basal cell spot on fore wing upperside very large, about twice as long as broad, much larger than central cell spot (fig. 6); on hind wing upperside median spots very conspicuous, median spot 1c running from vein 1b to vein 2 (*dromus* group) .... *wrefordi*
— Basal cell spot on fore wing upperside much smaller, rounded and not larger than central cell spot; median spots on hindwing upperside smaller or less

complete, median spot 1c rarely running from vein 1b to vein 2 24

24. Median spots on hind wing upperside incomplete, only 2 and 4—5 present and of the submarginal spots only 2 and 3 well developed, sometimes also 4 and 5 present as vague dots, very rarely a few white scales at place of submarginal spots 1b and 1c; median band on hind wing underside straight, outer margin finely dentate (spots slightly extended towards termen along veins) and along this margin ground colour darker (fig. 15) (*dromus* group) .. *secessus*

— On hind wing upperside median spots and usually also submarginal spots better developed; median band on hind wing underside more or less curved, outer margin not finely dentate nor contrasted by darkening of ground colour .. 25

25. On fore wing upperside inner median spots 1b and 1c well-developed, forming a bar from vein 1 to vein 2; outer median spot 1b absent, 1c a small dot at lower outer angle of median spot 2, or absent (fig. 9); median spots on upperside of hind wing fused into a continuous, characteristically curved white band; Ethiopian species (*dromus* group) .... *dromus*

— On fore wing upperside inner median spot 1b and outer median spot 1c well-developed, inner median spot 1c and outer median spot 1b absent (the latter rarely indicated as a white point close to the outer median spot 1c); median spots on hind wing upperside separated by ground colour along the veins; Oriental species (*sertorius* group) .... *galba*

Checklist of *Spialia* species

asterodia group	*asterodia*	*dromus* group	*wrefordi*
	agylla		*paula*
	kituina		*secessus*
spio group	*spio*		*dromus*
	diomus		*ploetzi*
phlomidis group	*phlomidis*		
	osthelderi	*delagoae* group	*mangana*
	geron		*nanus*
	doris		*delagoae*
colotes group	*colotes*		*zebra*
	confusa		*sataspes*
sertorius group	*mafa*		*depauperata*
	galba		
	sertorius		
	orbifer		

3. THE *SPIALIA* SPECIES

The species groups recognized in this paper are pretended to be monophyletic subdivisions of the genus. They are based largely on the male and female genitalia. When studying the genitalia it soon became evident that a number of evolutionary trends could be found in the genus *Spialia*, these trends being represented by apparently autapomorphous character conditions of certain parts of the male and female genitalia. The intricacy of the genitalia makes them much more convenient for the study of phylogenetic relationships than the wing markings. Indeed, within the genus *Spialia* the latter vary mainly in the presence or absence and relative development of the spots. The absence of a particular spot in various species is a poor indication (or no indication at all) of relationship, as the loss of a spot may occur more than once independently. The presence of an additional spot would be a better indication, but in *Spialia* this seems to be realized in a single case only.

Thus, the three species of the *spio* group of Higgins (1924), which was based on the absence of median spot 6 on the underside of the hind wing, had to be placed in three different species groups in this paper while a number of other species groups recognized by Higgins could be united. The result of basing the genus groups on genital characters is that the classification shows the (supposed) interrelationships of the groups, while the exclusive use of characters of the wing markings results in a number of groups of which the interrelationships are quite obscure.

This does not mean, of course, that all characters of the wing markings are useless for the classification and as will be shown below, the position of certain spots is, in this respect, much more important than their presence or absence.

The phylogenetic implications will be dealt with in Chapter 4.

In the following, descriptions are given of all species groups as to their external characters, male and female genitalia. In the descriptions of the species these general features of the relevant species groups have not been repeated. Thus when a species has been identified by means of the key, the characters of its genitalia can be found in the combination of the characters of the relevant species group and of the species concerned (and, of course, by reference to the figures).

a. The *asterodia* group

External characters. — Upperside of fore wing with basal cell spot; central cell spot nearer to discocellular spot than to basal cell spot; basal spots in spaces 9 and 10 usually present as two white streaks lying over the central cell spot; submarginal spots present, but sometimes very incompletely developed. Underside of hind wing with all median spots present, forming an irregular band more or less parallel to the termen or fused with the basal spots in spaces 7 and 8 to form a Y; submarginal spots 4 and 5 in line with the other submarginal spots. Male with a costal fold (not very conspicuous).

Male genitalia. — Uncus deeply incised; junction with tegumen slightly marked, no fenestrula. Gnathos dorsally joined to tegumen over short distance, ventrally unspined, well sclerotized, the left and right parts ventrally connected by a (sometimes very narrow) membrane. Fultura superior smooth. Anellus membranous. Juxta may be hairy. Aedeagus straight, surface smooth. Saccus relatively long. Costal process of valva large, strongly spined and heavily sclerotized, more or less detached from costa or even attached to cucullus. Cucullus without fold covering costal process.

Female genitalia. — Segment 8 with a single, large, dorsal sclerite, separated by a membranous gap from the ventral sclerotization that is continuous antevaginally, but shows a large postvaginal membranous gap. On distal edge of postvaginal membrane no spines observable. Ductus long and imperceptibly passing into bursa. Beginning of ductus may be sclerotized. Bursa without sclerotization. Papilla analis without basal lobe; apophysis posterior longer than papilla, sharply bent at conjunction with papilla.

Spialia asterodia (Trimen)

Pyrgus asterodia Trimen, 1864. — Trans. ent. Soc. London (3) 2 : 178 (Plettenberg Bay, Cape Province). Holotype (♂) in the British Museum (Nat. Hist.), London.

Note. Trimen twice described this species as new, the first time in the above mentioned paper, the second time (1866) in his book "Rhopalocera Africae Australis", Part II. In his first description Trimen quoted as type locality only "Cape Colony", in his second description he mentioned Plettenberg Bay. The type specimen is labelled as coming from the latter locality.

External characters (pl. 1 figs. 1, 2). — The pronounced characters of the *asterodia* group, especially the position of the central cell spot, make a confusion with species of other groups improbable. The characters mentioned in the key will suffice to distinguish *asterodia* from the other species of the group, but we may add that *agylla,* the only species likely to be confused with *asterodia,* is on the average smaller: *asterodia* ♂ 9.8—12 mm, *agylla* ♂ 9.2—10.5 mm.

Apart from variation in size there is a slight variation in the extension of the spots and the ground colour of the underside of the hind wing may be darkened along the white spots. According to Swanepoel (1953) the spring specimens (August) have a darker underside of the hind wing than summer specimens (January).

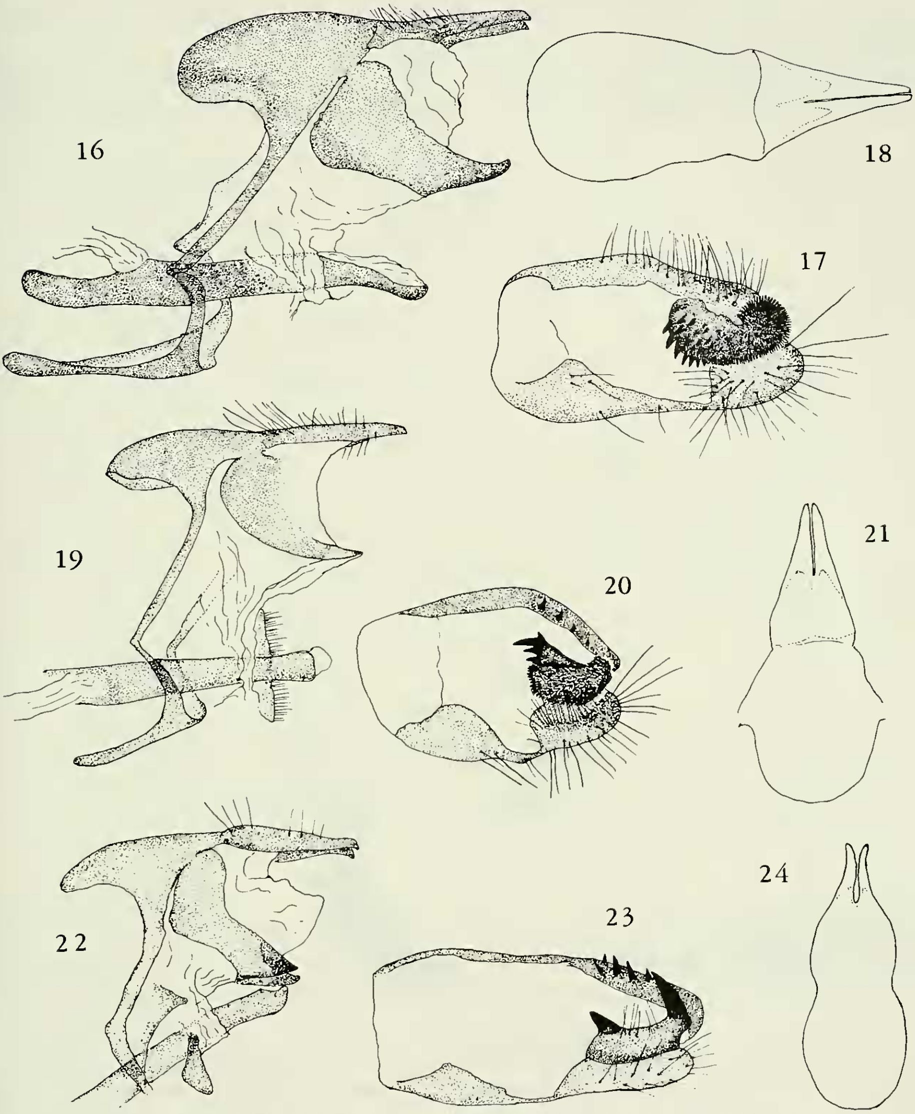
Male genitalia (figs. 16—18). — Two arms of uncus close together. Two parts of gnathos ventrally very close together. Costa of valva without spines. Costal process large, distally thickly beset with fine spines, more proximad the spines becoming larger and in the proximal part the spines coarse and large and directed downwards.

Female genitalia (figs. 25—27). — In addition to the group characters, the female of *asterodia* has the upper part of the ductus sclerotized. Antevaginal sclerotization appears slightly stronger than in *agylla.*

Ecology. — According to Swanepoel (1953) *asterodia* is a species of grasslands that ascends the Drakensberge to a height of more than 3000 m. It flies from August till March. Murray (1959) mentions as food plants various species of *Hermannia* (Sterculiaceae) and *Pavonia macrophylla* (Malvaceae).

Distribution (Map 1). — Confined to the southeastern part of Africa. In South Africa widely distributed through the southeastern, eastern and northeastern parts. Outside South Africa only known from Mozambique and Rhodesia.

Localities. — Rhodesia: Hillside (Bulawayo), Mashonaland, Salisbury (BM, NMB). Mozambique: Rikatla (24 km N of Lourenço Marques) (BM). South Africa. Cape Province: Addo, Assegaibosch, Brak River, Burghersdorp, Cape Town, Cathcart, Dordrecht, Grahamstown, Herd's Bay, Jefferey's Bay, Keurbooms River,

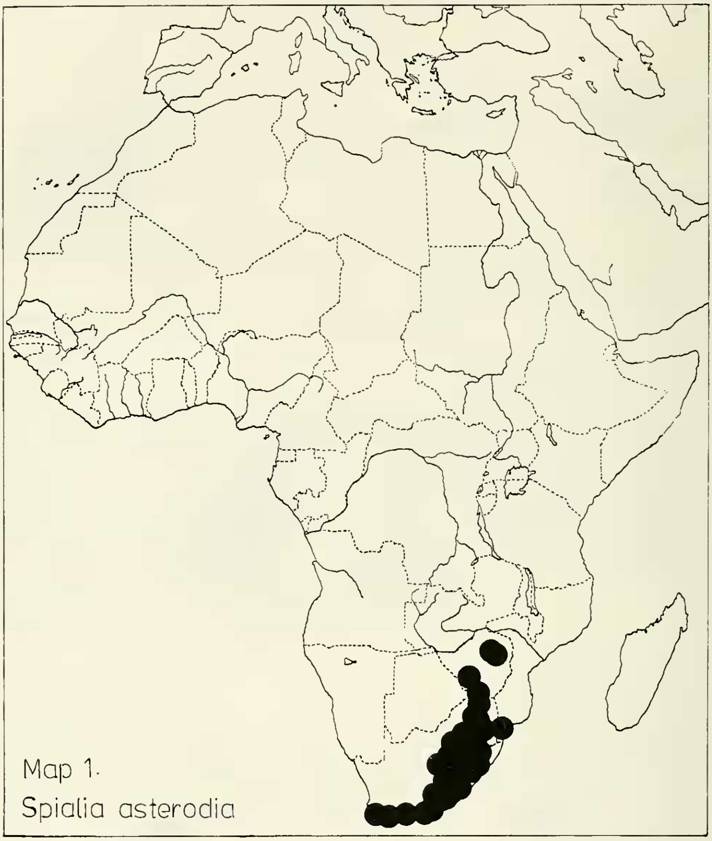


Figs. 16—24. Male genitalia, lateral aspect, valva, and dorsal aspect of tegumen and uncus. 16—18, *S. asterodia* (Natal). 19—21, *S. agylla* (Bloemfontein, S. Africa). 22—24, *S. kituina* (Voi, Kenya).

Kokstad, Plettenberg Bay, Port Elizabeth, Somerset East, Steynsburg, Swartkops, Swellendam (BM, CMP, MN, MNHN, NMB; Swanepoel, 1953). Orange Free State: Bethlehem, Bloemfontein, Kroonstad, Ladybrand, Lindley, Rouxville (MN, NMB; Swanepoel, 1953). Natal: Balgowan, Cleopatra, Estcourt, Greytown, Ladysmith, Loteni, Newcastle, Vrijheid (BM, MN, NMB; Swanepoel, 1953). Transvaal: Barberton, Ermelo, Graskop, Haenertsburg, Johannesburg, Lydenburg, Messina, Munnik, Pietersburg, Potchefstroom, Pretoria, Zoutpansberg (BM, CMP, NMB;

Swanepoel, 1953). Lesotho: Giant's Castle, Mamanthes, Maseru, Mokhotlong (NMB; Swanepoel, 1953).

Material examined. — 41 ♂, 35 ♀ : 39 ♂ (1 ♂ holotype), 34 ♀, South Africa (BM, CMP, MN); 1 ♂, 1 ♀, Mozambique (BM); 1 ♂, Rhodesia (BM).

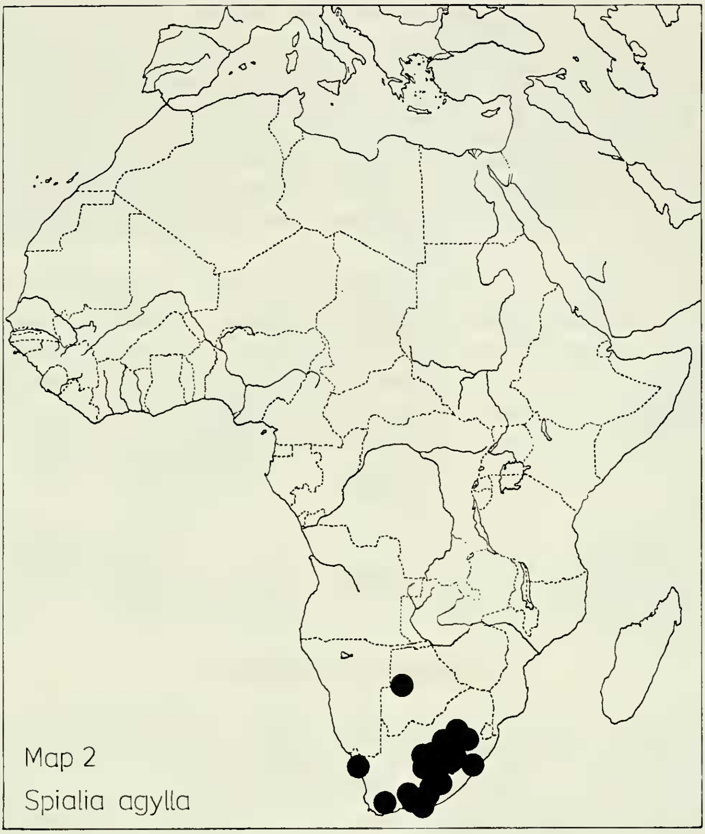


Spialia agylla (Trimen)

Pyrgus agylla Trimen, 1889. — South African Butterflies 3 : 286 (Griqualand West). See further under subspecies.

External characters (pl. 1 figs. 3, 4). — The characters mentioned in the key and under *asterodia* will suffice to distinguish this species. It varies in the same way as *asterodia*, but it is slightly smaller, ♂ 9.2—10.5 mm. One female in the BM has the median spot on the upper and underside of the hind wing much reduced. Swanepoel (1953) does not mention a seasonal variation.

Male genitalia (figs. 19—21). — Two arms of uncus less close together than in *asterodia*, more or less diverging. Two parts of gnathos ventrally clearly diverging. Costa of valva with spines in distal half along ventral edge. Costal process large,



more detached from costa than in *asterodia,* thickly beset with short spines of uniform length, with a dorsal, heavily sclerotized excrescence ending in a single very large spine, or one large and a few smaller spines, that all point towards the base of the valva (junction with vinculum) and not downwards.

Female genitalia (figs. 28, 29). — The only difference with *asterodia* seems to be a slighter sclerotization of the antevaginal region and the lack of sclerotization in the upper part of the ductus.

Ecology. — This species is found on mountains, mountain slopes and grassy plains, where it flies from August till April (Swanepoel, 1953). The food plants are said to be the same as for *asterodia* (Murray, 1959).

Distribution (Map 2). — Confined to southern Africa, where it is mainly found in the high uplands in the interior.

Geographic variation. — The recent discovery of this species in Namaqualand has led to the erection of a new subspecies. As the material of the new subspecies is limited and has been caught within three weeks, and as the differential characters are liable to environmental influences in other *Spialia* species, I consider the distinction of ssp. *bamptoni* tentative.

Spialia agylla agylla (Trimen)

Pyrgus agylla Trimen, 1889. — South African Butterflies 3 : 286 (Griqualand West, between Modder River and Riet River). Holotype (♂) in the British Museum (Nat. Hist.), London.

External characters. — Upper and underside of wings with size of spots more or less as in *asterodia*. Slightly larger than ssp. *bamptoni:* ♂ 9.2—10.5 mm.

Distribution. — The main range of the species, the uplands in the interior of South Africa. I also regard the specimens from Botswana as belonging to the nominate subspecies.

Localities. — South Africa. Cape Province: Aberdeen, Boschberg Mts, Burghersdorp, Cradock, Griqualand West, Hopetown, Kimberley, Klaarstroom, Matjesfontein, Murraysburg, Nauwpoort, Port Elizabeth, Queenstown, Somerset East, Steynsburg (BM, MN; Swanepoel, 1953). Orange Free State: Bethulie, Bloemfontein, Deelfontein, Ladybrand, Trompsburg (AMNH, BM, CMP, MN, MRAC; Swanepoel, 1953). Transvaal: Heidelberg, Johannesburg, Klipdrift, Standerton, Vaal River (BM; Swanepoel, 1953). Lesotho: Maseru, Leribe (Swanepoel, 1953). Botswana: Ghanzi (BM).

Material examined. — 38 ♂, 10 ♀ : 11 ♂ (1 ♂ holotype), 3 ♀, Cape Province (BM, MN); 25 ♂, 6 ♀, Orange Free State (AMNH, BM, CMP, MN, MRAC, NRS); 1 ♂, Transvaal (BM); 1 ♂, 1 ♀, Botswana (BM).

Spialia agylla bamptoni Vári

Spialia agylla bamptoni Vári, 1976. — Ann. Transvaal Mus. 30 : 123—124, figs. 3, 4, pl. 13 figs. 3, 4 (Hondeklipbaai, 1—18.xii.1974). Holotype (♂) in the Transvaal Museum, Pretoria.

External characters. — Spots on upper and underside of wings larger and more whitish than in ssp. *agylla,* ground colour of underside of hind wing also more whitish in the subbasal and submarginal areas. Slightly smaller than ssp. *agylla,* ♂ 9—10 mm.

Distribution. — Only known from the type-locality, Hondeklipbaai (Namaqualand Distr.) at the west coast of South Africa (Vári, 1976).

Material examined. — None.

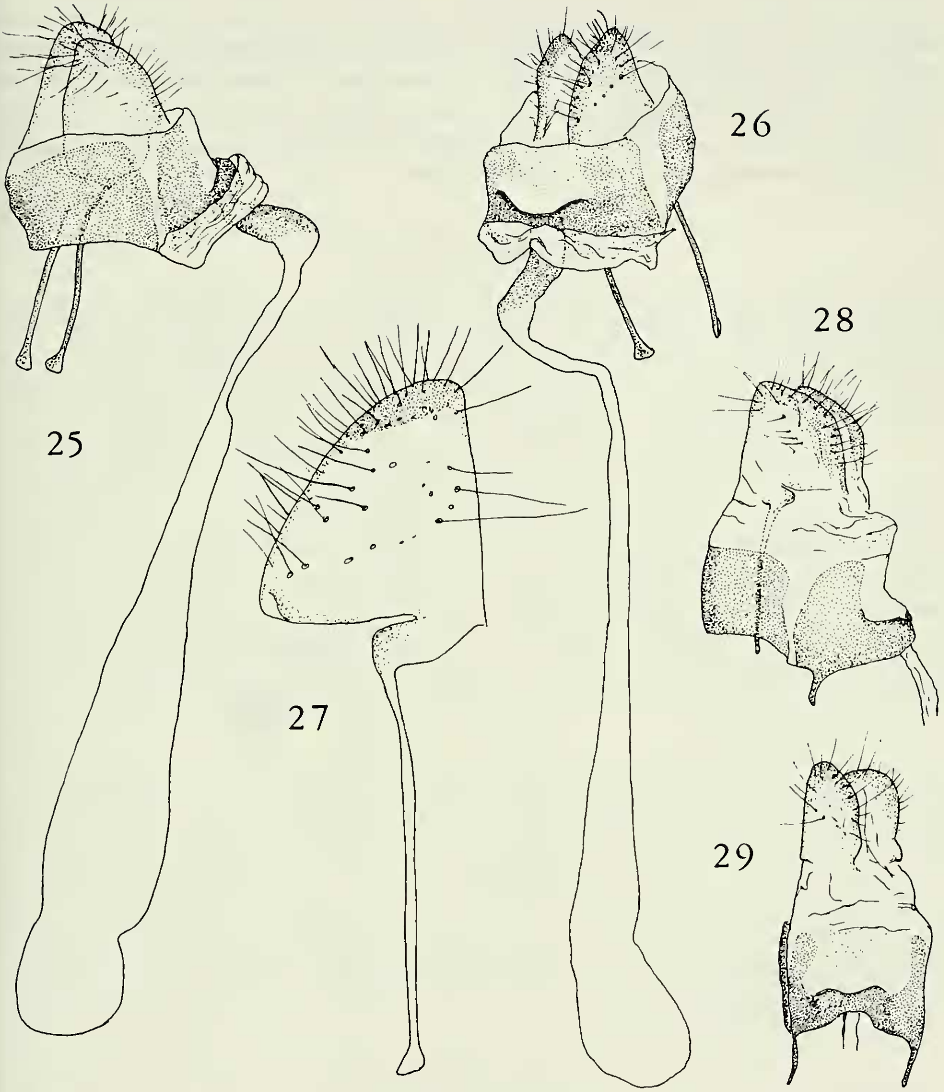
Spialia kituina (Karsch)

Hesperia kituina Karsch, 1896. — Ent. Nachr. 22 : 374—375 (Kitui, Kenya). Holotype (♂) in Zoologisches Museum der Humboldt Universität, Berlin.

Evans (1937) stated as type-locality "Zanzibar" and Dr. Hannemann kindly informed me that the type is labelled in the same way, but from Karsch' original description ("aus dem Sansibar-gebiete, von Kitui") it follows that the type-locality is not the present island of Zanzibar. At the time of Karsch the Sultanate of Zanzibar covered large parts of East Africa.

Pyrgus bettoni Butler, 1898. — Proc. zool. Soc. Lond. 1898 : 415, pl. 32 fig. 1 (Maungu Inkubwa, Kenya). Holotype (♂) in the British Museum (Nat. Hist.), London.

External characters (pl. 1 figs. 5, 6). — An unmistakable species. It has the position of the central cell spot, close to the discocellular spot, in common with *asterodia* and *agylla,* but it will at once be distinguished by the Y-shaped band on the underside of the hind wing. By this character it is also distinguished from all other *Spialia* species.

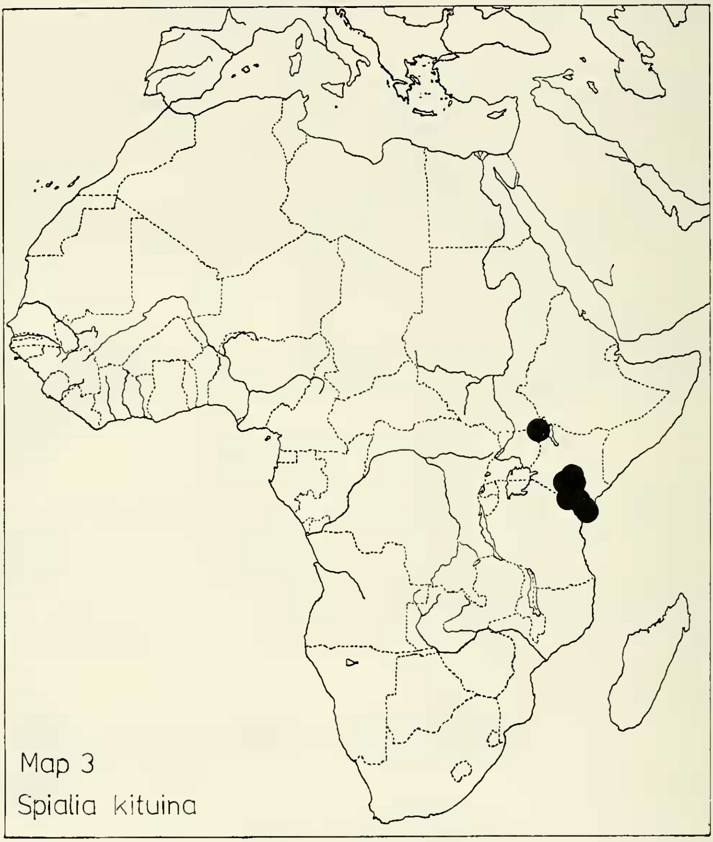


Figs. 25—29. Lateral and ventral aspect of female genitalia, and papilla analis. 25—27, *S. asterodia* (Natal). 28—29, *S. agylla* (Hopetown, S. Africa).

Male genitalia (figs. 22—24). — Higgins (1924) mentioned an undivided uncus, but in fact the uncus is deeply indented and the apices of the two parts diverge. Ventral parts of gnathos also diverging apically. Costa of valva with a few spines pointing upwards in the distal half. Costal process detached from costa, attached to undeveloped cucullus (at least, this process is supposed to be homologous with the costal process in the other *Spialia* species), strongly sclerotized, oblong, with a strong tooth at its proximal end and a very large tooth at its distal end protruding beyond the dorsal rim of the costa.

Higgins (1924) mentioned "elaborate interlocking terminal teeth". From his figure (pl. 9 fig. 1) it is clear that one of these teeth is the distal tooth of the costal process, while the other one is in fact the costa that is connected by a membrane (omitted in Higgins' figure) to the costal process.

Female genitalia. — Due to lack of material *kituina* is the only *Spialia* species of which the female genitalia could not be studied.



Ecology. — In the Shimba Hills (SE. Kenya) specimens have been found in January, February, July, August and November (Sevastopulo, 1974). Food plants unknown. I found this species together with *Spialia zebra* along a dry, hot road near Ukunda (S. of Mombasa) in a rather open, more or less cultivated terrain in the beginning of November.

Distribution (Map 3). — Confined to Kenya. Higgins (1924) stated that there is a specimen in the British Museum (Nat. Hist.) from British Central Africa, but I could not find that specimen. Neave (1910) recorded a number of specimens from the Luangwa Valley (Zambia), which he hesitatingly placed as the wet-season form of *"Hesperia bettoni"*. The only specimens in the Neave collection in the Hope Department, Oxford, that come into consideration belong to *Spialia confusa confusa*.

Localities. — Kenya: Bura (Teita), Diani, Kaitir, Kangondi, Kibwezi, Kitui, Landjoro (Pori), Lokichogio, Lukenia, Makueni, Maungu Inkubwa, Mombasa, Mulango, Shimba Hills (Kakardara and Marere Forests), Taveta, Ukambani, Ukazzi Hill (Garissa Rd), Ukunda, Voi (AMNH, BM, CMP, ML, MN, MNHN; Higgins, 1924; Karsch, 1896; Sevastopulo, 1974).

Material examined. — 21 ♂ (1 ♂ holotype of *bettoni*), 5 ♀, Kenya (AMNH, BM, CMP, ML, MN, MNHN).

b. The *spio* group

External characters. — Upperside of fore wing with basal cell spot; central cell spot midway between basal cell spot and discocellular spot; no spots in spaces 9 and 10; submarginal spots usually well-developed. Median spots on underside of hind wing complete, forming a continuous band, or median spot 6 absent; submarginal spots 4 and 5 in line with the other submarginal spots; an additional spot between the submarginal and median spots in space 1c. Male without costal fold.

Male genitalia. — Uncus undivided, junction with tegumen well-marked and with fenestrula or almost invisible. Gnathos free from tegumen by a very narrow membranous gap; dorsally broad, ventrally narrower and with some spines, distally very gradually passing into the more or less spinulose membrane that joins the left and right parts of the gnathos. Anellus membranous, spinulose or smooth. Aedeagus straight, without marked spines. Saccus slightly shorter than or about as long as uncus. Costal process of valva a strongly spined structure in central part of costa or a finger-like excrescence of dorso-distal part of costa. Cucullus spined dorso-distally.

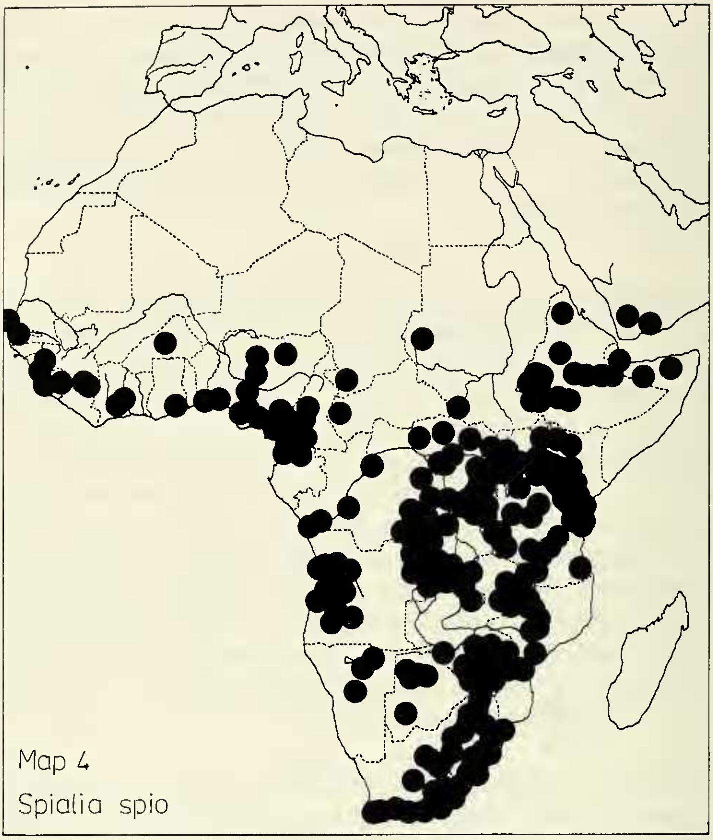
Female genitalia. — Segment 8 with two dorsal sclerites that extend far laterally; ventrally a single sclerite or two sclerites separated by a narrow membranous gap distally of the ostium. In the distal part the ventral surface bears a membranous or sclerotized flap that partly overlaps the spinulose area. This area is well-developed and not connected to the ventral sclerite(s). Antevaginally there is a strong sclerotization which may be divided into a left and right part, recalling the sclerotized "wings" in the *phlomidis* group. Upper part of ductus may be sclerotized. Bursa without sclerotizations. Papilla analis with basal lobe; apophysis posterior long, longer than papilla.

Spialia spio (Linnaeus)

Papilio spio Linnaeus, 1767. — Syst. Nat., Ed. XII, 1 (2) : 796 (Cape of Good Hope). Of the type only figures exist. Linnaeus referred to figures by Clerck, which were not published before 1882, when Aurivillius reproduced them. Only then it could be determined that the poor description by Linnaeus referred to the species that was generally known as *Papilio vindex* Cramer, 1782. Although this synonymy is undoubtedly correct, the figures of Clerck reproduced by Aurivillius are so bad as to lead Oberthür (1912) to consider *spio* and *vindex* separate species.

Papilio vindex Cramer, 1782. — Cramer, Uitlandsche Kapellen 4 : 122, pl. 353 figs. G, H (Cape of Good Hope). Type presumably lost.

External characters (pl. 1 figs. 7, 8). — A variable species, that is, however, usually not difficult to distinguish. To the characters mentioned in the key we may add the following notes. In rare cases the median spot 6 on the underside of the hind wing is faintly developed. The additional spot in space 1c on the underside of



the hind wing is not always well-developed. A useful distinguishing character can also be found on the upperside of the hind wing, where the submarginal spots 4 and 5 are fused to form a single large conspicuous spot in most specimens; this spot usually distinguishes *spio* from all other *Spialia* species.

From the two other widely distributed and common *Spialia* species in Africa, viz., *dromus* and *diomus, spio* is easily distinguished by the development of the median spots in space 1b on the upperside of the fore wing (figs. 7—9). In *spio,* inner median spot 1b and outer median spot 1c are always present and subequal, the other median spots in space 1b are absent. In *dromus* the inner median spots 1b and 1c are always both present and usually fused, outer median spot 1c is very small or absent, outer median spot 1b is always absent. In *diomus* the inner median spot 1b is present, but usually small, inner median spot 1c is always absent, the outer median spots 1b and 1c are always both present and usually fused. In other words, on the upperside of the fore wing, there is no white bar in space 1b extending from vein 1 to vein 2 in *spio,* such a bar is present and composed of the inner median spots in *dromus* and also present but composed of the outer median spots in *diomus*.

Further differences are the following. On the upperside of the hind wing median spot 6 is always absent in *spio* (in very few specimens represented by a few white scales), usually present but faintly developed in *diomus* and usually present as a clear spot in *dromus*. The series of submarginal spots on the upperside of the fore wing is much more sinuous in *dromus* (especially in spaces 2 and 3) than in *spio* and *diomus*. The black bar in the fringes of the fore wing at the end of vein 5 is always well-developed in *dromus,* variable, but often narrow in *diomus* and narrow or (in most cases) absent in *spio*.

There is a large variation in size, the males varying from 8.7 to 13.0 mm; in the development of the spots and in the ground colour of the underside of the hind wing, which varies from pale yellow to dirty green. In addition, there exists some variation in the wing shape. Usually the fore wings of the males are slightly more pointed than those of the females, but males with rounded and females with pointed wings also occur. Probably, temperature and humidity are largely responsible for these varieties. The described variation is not geographical.

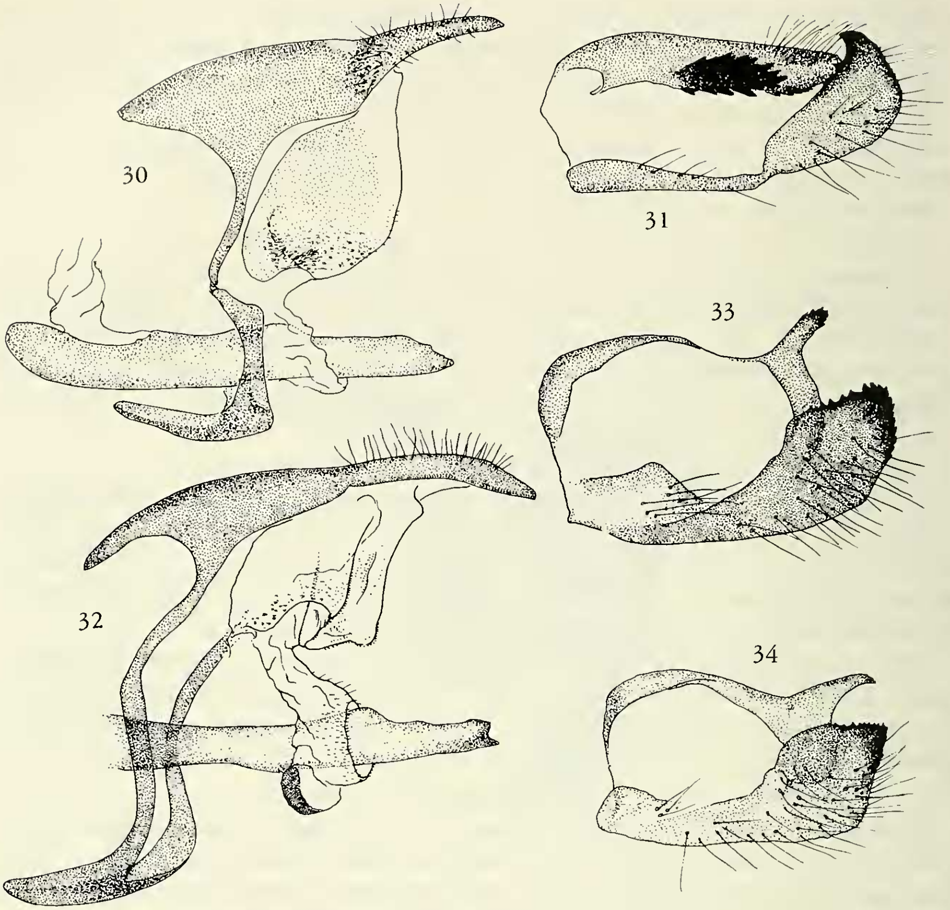
Male genitalia (figs. 30, 31). — A large fenestrula at junction of uncus and tegumen. Gnathos free from tegumen, distally gradually passing into fultura superior, which bears some small spines, ventrally forming a more or less triangular, slightly spined "head". Anellus membranous, smooth. Costal process of valva a strongly spined structure near the centre of the costa. Cucullus dorso-distally pointed, strongly sclerotized and with a strong tooth near the junction with the costa.

Female genitalia (figs. 35, 36). — Ventral sclerotization of segment 8 forming a single, not sharply defined sclerite with a sclerotized projecting flap that partly overlaps the area spinulosa which is pointed distally. Antevaginally with two strongly sclerotized and folded, wing-like structures. Papilla analis with small basal lobe, that scarcely covers the base of the apophysis posterior.

Ecology. — Although in South Africa *spio* is a species of open grounds (Swanepoel, 1953), at least in East Africa it seems to prefer fringes of dense scrub, sometimes occurring along forest paths (own observations; experiences of my friend, Mr. J. H. Lourens). Probably, it is a rather adaptable species, that can live where the vegetation structure is not too dense (closed forest) or too open (subdesert, desert). It may fly almost throughout the year, but this depends on local conditions. Recorded food plants are several *Hermannia* species (Sterculiaceae) and *Pavonia macrophylla* and *columella* (Murray, 1959), *Hibiscus aethiopicus* (Gifford, 1965), and *Sida* (Van Someren, 1939) (all Malvaceae).

Distribution (Map 4). — One of the most widely distributed African *Spialia* species, occurring throughout the Afrotropical Region in suitable habitats and penetrating the Arabian peninsula in the extreme south. Although the species is not known from large areas, this often appears to be the result of undercollecting rather than of true absence.

Localities. — Yemen: Wadi Dhar (6 mls NW of San'a) (BM; Gabriel, 1954). South Yemen: Hadramaut (BM). Somalia: Buran, 40 mls S of Buran, Holl-Holl (MN, MNHN; Talbot, 1932). Sudan: Bamaka, Jebel Marra (Darfur), Niurnya (BM). Ethiopia: throughout (BM, MNHN; Carpenter, 1935). Kenya: throughout (AMNH, BM, CMP, ML, MN, MNHN, NMB, USNM, ZSM). Uganda: throughout (AMNH, BM, CMP, ML, MN, MRAC). Tanzania: throughout (BM, ML, MN,



Figs. 30—34. Male genitalia, lateral aspect, and inside of right valva. 30—31. *S. spio* (S. Africa). 32—33, *S. diomus ferax* (Pretoria, S. Africa). 34, *S. diomus diomus* (Ukunda, Kenya).

MNHN, MRAC, ZSM; Aurivillius, 1910). Ruanda: Cyangugu, Rugege Forest (Lake Kivu) (BM, ML). Burundi: Butoni, Kibimba, Kitega, Misumba, Usumbura (MRAC). Malawi: throughout (BM, MNHN, NMB; Gifford, 1965). Zambia: Chingola, Fort Jameson, Kabompo River, Mid Luangwa Valley, Upper Luangwa Valley (BM, NMB). Rhodesia: throughout (MN, MNHN, NMB, USNM). Mozambique: Augustino Farm (Revue River), Delagoa Bay, Inhanucarara, Serra Rotanda, Siluve (Xiluvo) Hills (BM, MNHN, NMB, ZSM). Swaziland: Gollel (NMB). South Africa: throughout (AMNH, BM, CMP, ML, MN, MNHN, MRAC, NMB, USNM, ZSM; Swanepoel, 1953). Botswana: Kwaai River, Maun, 55 mls E of Maun, 25 mls E of Tsane (NMB). Namibia: Grootfontein, Okahandja, Omaramba-Oamatako (SMW; Trimen, 1891). Angola: Banga, Barraca (Quanza River), Benguela, Biho Distr., between Capelongo and Dongo, Cassualalla, Cubal River, Gauca, Huambo, Kuvali River, N'Dalla Tando, Omrora, Pacolo (Luanda), Pungo Adongo (BM, CMP, ML, MNHN; Trimen, 1891). Zaïre: throughout (AMNH, BM, CMP, MN, MNHN, MRAC, NMB, ZSM). Congo-Brazzaville: Fort Crampel (MNHN). Gabon: Oyem (MNHN). Rio Muni: Makomo Campo (ZSM). Central African Rep.: Boukoko M'Baiki, Oubangui (MNHN, MRAC). Chad: Bebedjia (Moundou) (ML). Cameroun: throughout central and southern parts (BM, CMP, MNHN, USNM). Nigeria: Afikpo, Akassa to Onitsha, Fumban, Kano, Lagos, Lokoja, Lower Niger, Ogruga, Zaria, Zungeru (NMB, BM). Dahomey: Porto Novo (MNHN). Ghana: Accra, Likpe, Gold Coast (BM, MRAC, USNM). Upper Volta: Pundu (ZSM). Ivory Coast: Bayota Forest (Gagnoa), Dimbokro (BM, MN). Liberia: Monrovia (Holland, 1896). Sierra Leone: Benikoro, Freetown, Sefadu, Yiraia (BM, ML, ZSM). Guinea: Conakry, Dalaba, Macenta, N'zérekoré (BM, MNHN). Gambia: Gambia (BM). Senegal: Dakar, Niokola Koba (BM, MNHN; Condamin, 1969).

Material examined. — 692 ♂, 384 ♀ : 1 ♂, Yemen (BM); 1 ♂, S. Yemen (BM); 3 ♂, Somalia (MN); 16 ♂, 9 ♀, Ethiopia (BM, MN); 3 ♂, 2 ♀, Sudan (BM); 82 ♂, 63 ♀, Kenya (AMNH, BM, CMP, ML, MN, USNM, ZSM); 37 ♂, 22 ♀, Uganda (AMNH, BM, CMP, ML, MN, MRAC); 106 ♂, 54 ♀, Tanzania (BM, ML, MN, MRAC, ZSM); 1 ♀, Ruanda (ML); 21 ♂, 7 ♀, Burundi (MRAC); 12 ♂, 9 ♀, Malawi (BM); 3 ♂, 2 ♀, Zambia (BM); 3 ♂, Rhodesia (MN, USNM); 9 ♂, 3 ♀, Mozambique (BM, ZSM); 110 ♂, 79 ♀, South Africa (AMNH, BM, CMP, ML, MN, MRAC, USNM, ZSM); 2 ♂, 2 ♀, Namibia (SMW); 10 ♂, 3 ♀, Angola (BM, CMP, ML); 204 ♂, 81 ♀, Zaïre (AMNH, BM, CMP, MN, MRAC, ZSM); 1 ♀, Rio Muni (ZSM); 1 ♂, Centr. Afr. Rep. (MRAC); 1 ♂, 1 ♀, Chad (ML); 41 ♂, 30 ♀, Cameroun (BM, CMP, USNM); 11 ♂, 6 ♀, Nigeria (BM); 2 ♂, 2 ♀, Ghana (BM, MRAC, USNM); 1 ♂, 1 ♀, Ivory Coast (BM, MN); 10 ♂, 4 ♀, Sierra Leone (BM, ML, ZSM); 1 ♂, 2 ♀, Guinea (BM); 1 ♀, Gambia (BM); 2 ♂, 1 ♀, Senegal (BM).

Spialia diomus (Hopffer)

Pyrgus diomus Hopffer, 1855. — Monatsber. K. Akad. Wiss. Berlin 1855 : 643 (Mozambique). For synonymy, see subspecies.

External characters (pl. 2 figs. 9—12). — An unmistakable species, distinguished by the following combination of characters:

1. On the upperside of the fore wing the outer median spots 1b and 1c are both present, forming a bar that extends from vein 1 to vein 2; inner median spot 1b present, 1c absent; submarginal spots well-developed; basal cell spot present (fig. 8).
2. On the underside of the hind wing the median band is entire, not broken at space 6. See also under *Spialia spio*.

Apart from the characters of the wing pattern *diomus* can be distinguished from all other *Spialia* species by the presence of spines on the mid-tibiae (besides the apical pair of spines).

There is a marked variation in the ground colour of the underside of the hind wing, from bright creamy yellow to deep olive-brown (sometimes dirty green). (See further under Geographic variation).

Male genitalia (figs. 32—34). — No fenestrula at junction of uncus and tegumen.

Gnathos free from tegumen, distally passing gradually into a finely spinulose, folded fultura superior, ventrally without differentiated "heads". Anellus membranous, spinulose. Costal process of valva a finger-like projection of the dorso-distal part of the costa. Cucullus strongly spined dorso-distally (with serrated edge).

Female genitalia (figs. 37, 38). — Ventral sclerotization of segment 8 consisting of two sclerites separated by a membranous region along the midline of the segment; tongue-like flap membranous, partly overlapping the area spinulosa, which is not pointed distally. Ventrally of the ostium there is a strongly sclerotized, irregular antevaginal plate. Papilla analis with a large basal lobe, covering half of the base of the papilla and the whole base of the apophysis posterior.

Ecology. — In many parts of its range a common species on open grounds. Swanepoel (1953) even states: "You cannot wander over the South African veld without meeting *diomus* almost everywhere . . .". In more or less forested areas *diomus* is scarce or absent and from own experience I think that it is much more confined to open grounds than *spio*.

S. diomus may be found throughout the year where it is not too dry or too cold seasonally. Recorded food plants are various species of *Hermannia* (Sterculiaceae) and *Pavonia macrophylla* (Malvaceae) (Murray, 1959).

Distribution (Map 5). — Distributed throughout the Ethiopian region where open grounds occur, but lacking in the extensively forested areas in the central and western parts of the Ethiopian region. Possibly continuously distributed from South Africa through Mozambique and Tanzania to Ethiopia, Sudan and Yemen. The apparent gap in the known distribution in Malawi and Mozambique may be due to undercollecting rather than to real absence. The same holds for the savanna-belt from Sudan to West Africa, where *diomus* is unknown from large regions, presumably as a result of incomplete exploration. Although I have seen specimens from various parts of West Africa, *diomus* was recorded neither by Berger (1962) from Guinea and Ivory Coast, nor by Lindsay & Miller (1965) from Liberia.

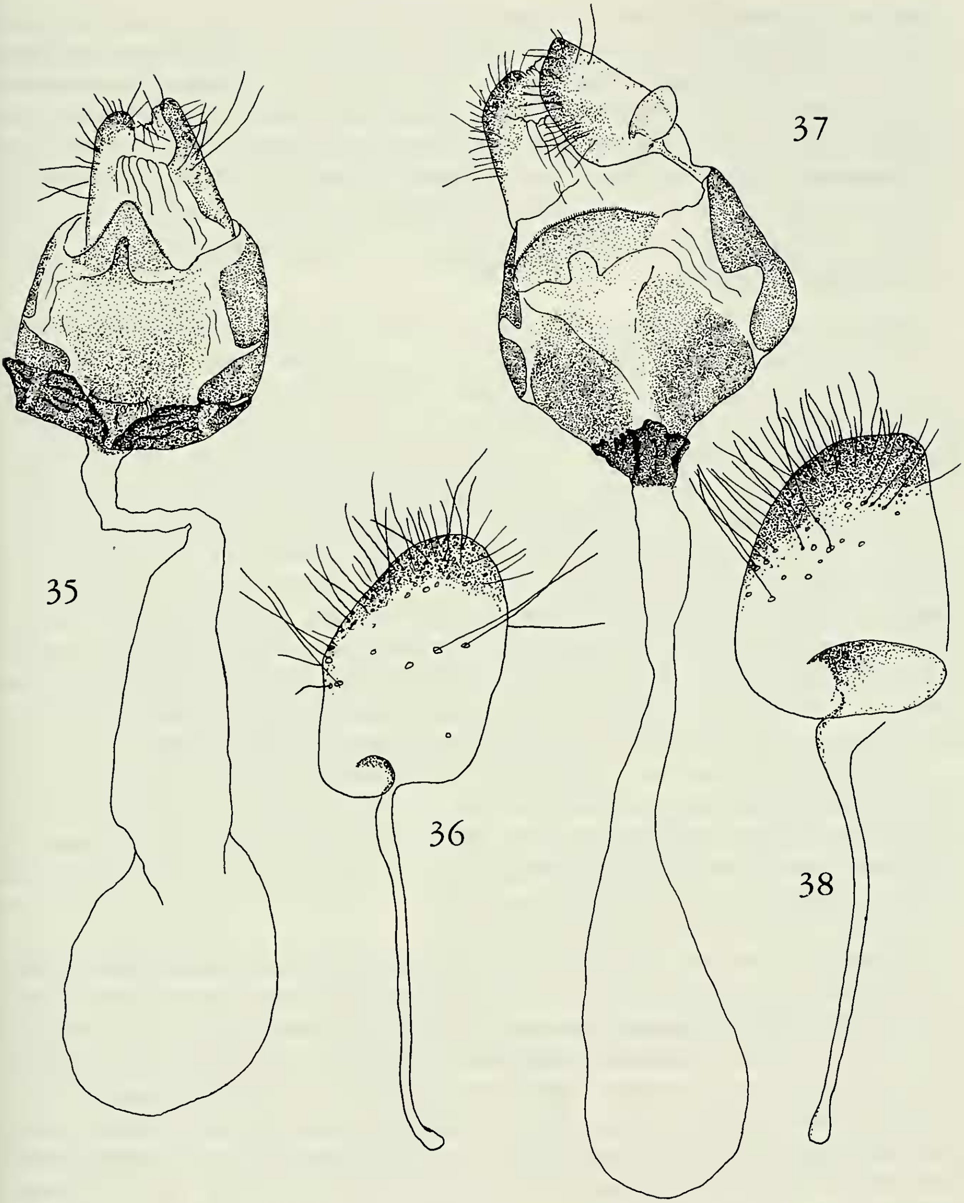
Geographic variation. — There is a marked difference between the forms found in the southern parts of Africa and in the rest of the Ethiopian region. The contact zone is obscure by lack of data, but may be running through Zambia, Malawi and Central Mozambique. The differences are found in the wing markings and male genitalia. Some authors (e.g. Oberthür, 1912; Higgins, 1924) regarded the differences too large to unite the forms into a single species, but a close examination reveals that the difference in the wing markings is not as large as would appear at first sight. But apart from this, there is no need for a specific separation as there is no evidence for geographic overlap of these forms.

Spialia diomus diomus (Hopffer)

Pyrgus diomus Hopffer, 1855. — Monatsber. k. Akad. Wiss. Berlin 1855 : 643 (Mozambique). The type appears to be lost; it is not in the Zoologisches Museum der Humboldt-Universität, Berlin.

Pyrgus machacoana Butler, 1899. — Proc. zool. Soc. London 1899 : 426, pl. 25 (Machakos, Kenya). Holotype (♂) in the British Museum (Nat. Hist.), London.

External characters (pl. 2 figs. 9, 10). — The main difference with ssp. *ferax* is found on the underside of the hind wing, where the median band is directed



Figs. 35—38. Female genitalia, ventral aspect, and papilla analis. 35—36, *S. spio* (Natal). 37—38, *S. diomus ferax* (Mozambique).

towards mid-dorsum by a strong curve of the band in space 2, caused by a shift of median spot 2 towards the base of space 2; median spot 1c is well-developed, but usually free from median spot 2, the additional spot in space 1c is well-developed, usually larger than the median spot, sometimes connected to median spot 2, but usually separated by dark scales along vein 2; the median band is broad in its upper part, especially in space 8 where it may almost touch the basal spot. The series of submarginal spots on the underside of the hind wing is more strongly curved and more irregular than in ssp. *ferax,* leaving a narrow, light-coloured region between the submarginal spots and the termen. The differences between the subspecies found on the underside of the hind wing are only weakly reflected on the upperside: only the shift of median spot 2 towards the wing base in ssp. *diomus* is usually visible, but this shift is sometimes also found in ssp. *ferax*.

Male genitalia (fig. 34). — The cucullus is broader and dorsodistally more pointed than in ssp. *ferax*.

Distribution. — The northern part of the range of the species, from West Africa to Ethiopia and Yemen. The southern limit is not exactly known, it may run through Zambia and Central Mozambique. In Mozambique ssp. *ferax* is known from the extreme south only, while the holotype of *diomus* originated from Mozambique. Lindsey & Miller (1965) concluded from the fact that Evans (1937) classified all material from Mozambique in the British Museum (Nat. Hist.) as ssp. *ferax,* while the type-locality of ssp. *diomus* is also Mozambique, that the correct name for the northern populations should be *machacoana,* "unless there is evidence that Hopffer's type was mislabelled geographically". As Hopffer clearly described and figured (Hopffer, 1862) the same form as *machacoana,* the name *diomus* cannot be replaced by *machacoana,* the latter being the junior synonym. Moreover, as all material of ssp. *ferax* in the British Museum (Nat. Hist.) originates from the extreme south, and the length of Mozambique (north-south) is about 2000 km, there is no reason to suppose that the type of ssp. *diomus* was mislabelled.

It is unfortunate that the species is not yet known from Malawi (Gifford, 1965), as it would be interesting to know whether ssp. *diomus* or an intermediate form occurs there. From Tanzania only ssp. *diomus* is known. Neave (1910) recorded *"Hesperia diomus* Hpff." from Zambia, but the two specimens from his collection (HDE) studied turned out to belong to ssp. *ferax*.

Localities. — Yemen: Hada (Gabriel, 1954). South Yemen: Aden, Dhala, Jebel Jihaf, Lahej, Laudar, Wadi Dareija (BM; Gabriel, 1954). Somalia: Gala River, Upper Sheikh (BM). Ethiopia: throughout (BM, MN, MNHN, MRAC; Carpenter, 1935). Sudan: Bahr-el-Ghazal, Darfur Prov., Dilling Forest Reserve, Gondokoro (White Nile), Kulme, Kurmuk (BM, MN). Kenya: throughout (AMNH, BM, CMP, ML, MN, MNHN, NMB, USNM, ZSM; Sevastopulo, 1974). Uganda: Arua, between Jinja and Busia, Busoga, Kafu River, Kakindu, Kampala, Kotido, Madi Opei, Metu Hills, Mtanda (AMNH, BM, NM, USNM). Tanzania: Dar es Salaam, Iringa, Kasulu, Katoto, Kifumbu, Kilema, Kilimanjaro West, Kiloa, Lake Manyara, Moshi, Mpapura, Mwanza, Ngorongoro, Pemba, Rulenge, Tange, Ukerewe, Usambara, Zanzibar (BM, ML, MN, MNHN, NMB, ZSM). Burundi: Kitega (MRAC). Zaïre: Kadjuju, Luna River, Nioka, Nyamunyunye, Rutshuri to Kabali, Usumbura to Schangugu (BM, MNHN, MRAC). Chad: Bebedjia (Moundou), Fort Archambault (ML, MNHN). Nigeria: Bida, Farniso, Kano, Lagos, Muri Prov., O'okemeji, Wurkum, Yelwa (BM). Upper Volta: Pundu (ZSM). Liberia: Zorzor (CMP). Guinea: Kouroussa, N'zérékoré (BM, MNHN). Gambia: Gambia (BM).

Senegal: Einaye, Melon à Kaolack, Oussouye Sandiala, Tabi près Bignona (BM, MNHN; Berger, 1968).

Material examined. — 134 ♂, 67 ♀ : 4 ♂, 1 ♀, South Yemen (BM); 1 ♂, 1 ♀, Somalia (BM); 9 ♂, 4 ♀, Ethiopia (BM, MN, MRAC); 5 ♂, Sudan (BM, MN); 56 ♂, 28 ♀, Kenya (AMNH, BM, CMP, ML, MN, USNM, ZSM); 10 ♂, 4 ♀, Uganda (AMNH, BM, MN, USNM); 22 ♂, 8 ♀, Tanzania (BM, ML, MN, ZSM); 11 ♂, 9 ♀, Burundi (MRAC); 5 ♂, 1 ♀, Zaïre (BM, MRAC); 4 ♂, 2 ♀, Chad (ML); 3 ♂, 5 ♀, Nigeria (BM); 1 ♀, Upper Volta (ZSM); 1 ♀, Liberia (CMP); 1 ♂, 1 ♀, Guinea (BM); 1 ♂, Gambia (BM); 2 ♂, 1 ♀, Senegal (BM).

Spialia diomus ferax (Wallengren)

Syrichtus ferax Wallengren, 1863. — Wien. ent. Monatschr. 1863: 137 (Kuisip River). Holotype (♂) in the Naturhistoriska Riksmuseet, Stockholm. The type-locality is generally known as the Kuiseb River, south of Swakopmund (Namibia).

The name was misspelled *"ferox"* by Holland (1896) and Oberthür (1912).

Pyrgus abscondita Plötz, 1884. — Mitt. naturw. Ver. Neu-Vorpomm. 15 : 21 (Africa). Type lost.

Higgins (1924), who treated *diomus* and *ferax* as distinct species, considered *abscondita* a synonym of *diomus*. This is, however, not in accordance with the rather bad reproduction of Plötz's figure by Aurivillius (1925). Evans (1937) treated *abscondita* as a senior synonym of *depauperata*. This cannot be correct, as Plötz mentioned a basal spot on the upperside of the hind wing, which is rarely or never present in *depauperata*. Moreover, the reproduction of Plötz's figure by Aurivillius (1925) shows the band of submarginal spots on the underside of the hind wing extending to the end of vein 8, while in *depauperata* it expires on the end of vein 7, and the median band in its upper part placed more basad than in *depauperata*, rather like *diomus ferax*.

Syrichthus lacreuzei Oberthür, 1912. — Et. Lép. Comp. 6 : 117, fig. 1332 (Zoutpansberg, South Africa). Holotype (♂) in the British Museum (Nat. Hist.), London.

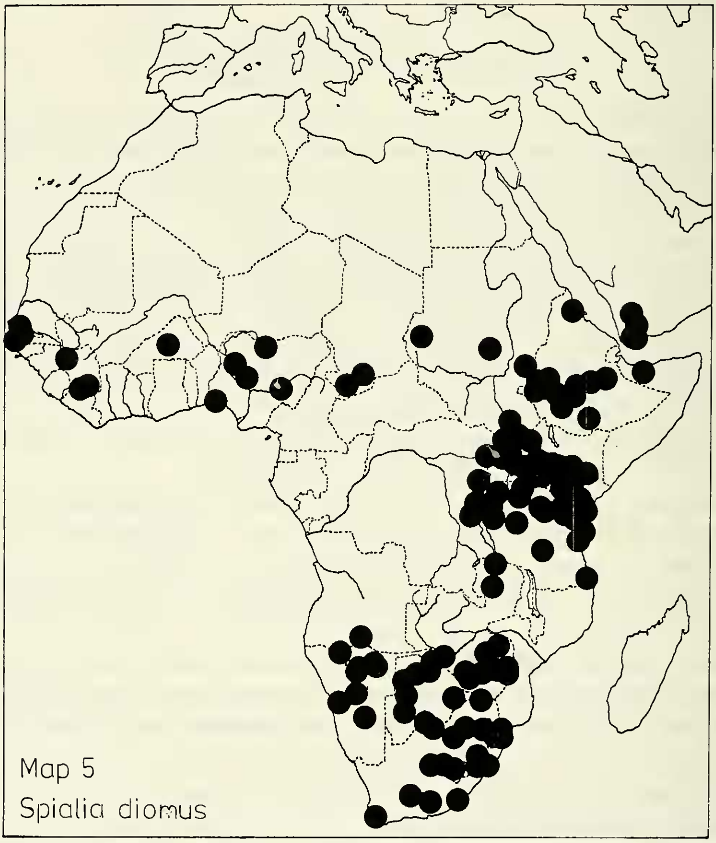
External characters (pl. 2 figs. 11, 12). — Median band of hind wing underside more regular, less broadening in its upper part and straighter than in ssp. *diomus*, directed towards tornus; median spot 2 in line with median spot 3 and connected with the additional spot in space 1c, which is obliquely extended towards the tornus; median spot 1c usually present, but weakly developed and free from median spot 2. Series of submarginal spots on the underside of the hind wing straighter and more regular than in ssp. *diomus;* the light-coloured area between the submarginal spots and the termen is narrow near the tornus, but broadens conspicuously towards the apex and is widest in space 6. See further under ssp. *diomus*.

Male genitalia (figs. 32, 33). — The cucullus is narrower, more rounded and more strongly spined than in ssp. *diomus*.

Distribution. — Southern Africa, north to Zambia and possibly Central Mozambique.

Localities. — Zambia: mouth Chambezi to Mansya River and Lake Young, high plateau S of Lake Tanganyika (HDE; Neave, 1910). Rhodesia: Buhera, Bulawayo, Matetsi, Mtoko, Mutambara, Nyamandhlovu, Salisbury, Selukwe, Strathmore Ranch (BM, CMP, MN, NMB). Mozambique: Delagoa Bay, Lourenço Marques, Shinawane (Xinavane) (BM, ML, MNHN, SMW, ZSM; Hopffer, 1855). Swaziland: Stegi (NMB). South Africa: throughout (AMNH, BM, CMP, ML, MN, MNHN, MRAC, NMB, NRS, USNM, ZSM; Swanepoel, 1953). Botswana: Kachikau, Kang Rd, 80 mls W of Kanye, Mafeking, Mahalapye, Maun, Nxai Pan, Okavango, Okwa, Sepopa, Tsane, Tsau (NMB, ZSM). Namibia: Kalidona, Kalkrand, Kano vlei, Kuiseb River, Okahandja, Omaramba-Oamatako, Otawi, Ovamboland, Tsumele (NMB, NRS, SMW, ZSM; Trimen, 1891; Wallengren, 1863). Angola: Ehanda (Trimen, 1891).

Material examined. — 92 ♂, 56 ♀ : 2 ♂, Zambia (HDE); 3 ♂, 1 ♀, Rhodesia (BM, CMP, MN); 5 ♂, 9 ♀, Mozambique (BM, ML, SMW, ZSM); 72 ♂, 44 ♀, South Africa (AMNH, BM, CMP, ML, MN, MRAC, NRS, USNM, ZSM); 1 ♂, Botswana (ZSM); 9 ♂, 2 ♀, Namibia (NRS, SMW, ZSM).

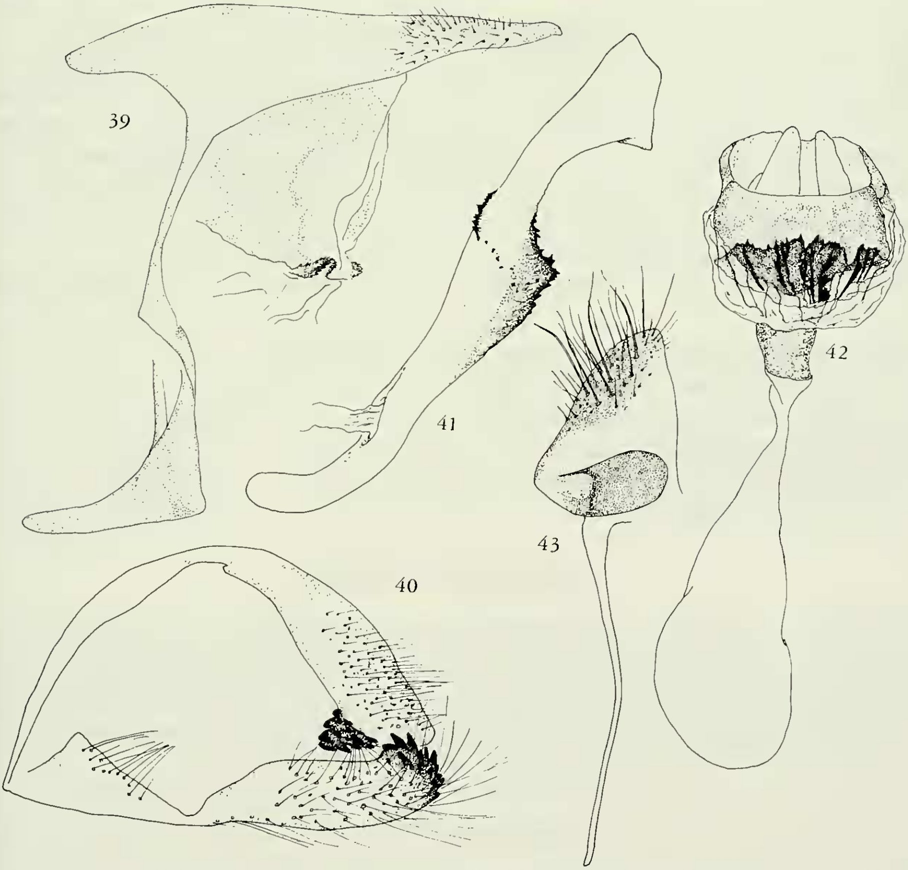


c. The *phlomidis* group

External characters (pl. 3). — Fore wing with basal cell spot on the upperside usually present, but vaguely outlined; central cell spot midway between basal cell spot and discocellular spot; submarginal spots usually all present and well-developed. On underside of hind wing usually all median spots present, but in most cases spot 6 not connected to inner or outer spot in space 7; submarginal spots 4 and 5 in line with the other submarginal spots. Male without costal fold.

Male genitalia (figs. 39—41). — Uncus undivided, junction with tegumen well visible but without fenestrula. Gnathos free from tegumen, dorsally broad, ventrally tapering to a small "head"; left and right part of gnathos joined by a more or less folded, usually finely spinulose membrane (fultura superior). Anellus membranous. Aedeagus with a strongly sclerotized and indented crest, latero-ventral in the middle, or a long, unindented branch in the same place, and with an extended apex. Saccus slightly shorter than uncus. Costa of valva broadening distally, in most species spined dorsally; costal process usually present as a ventrodistal excrescence of costa with strong spines. Cucullus spined dorso-distally, without fold covering part of the costal process.

Female genitalia (figs. 42, 43). — Segment 8 with two dorsal sclerites and two large ventral sclerites, which occupy the larger part of the ventral surface or are fused to a single large ventral sclerite. At the distal edge of the ventral side of segment 8 the area spinulosa may be visible. To the left and right of the ostium there is a heavily sclerotized and indented wing-like structure at the base of the segment. Ductus rather short, sclerotized in its upper part, rapidly broadening to



Figs. 39—41. Male genitalia, lateral aspect, aedeagus, and inside of right valva of *S. phlomidis* (Turkey). Figs. 42—43. Female genitalia, lateral aspect, and papilla analis of *S. phlomidis* (Greece).

the oblong bursa, which does not bear any ornamentation. Papilla analis with basal lobe; apophysis posterior long, longer than papilla.

Identification. — *S. doris* is the only species of the *phlomidis* group that by its distribution can be confused with African *Spialia* species (especially *mafa* and *spio*, by the absence or poor development of median spot 6 on the underside of the hind wing), as *doris* penetrates the Afrotropical region in Sudan, Ethiopia, Somalia and Kenya. It is, however, recognized on the upperside of the fore wing by the vague outline of the basal cell spot and the usual presence of both outer median spots 1b and 1c (in *mafa* and *spio* the outer median spot 1b is always absent) and on the underside of the hind wing by the presence of a small median spot 6.

Note. — The species of the *phlomidis* group *(phlomidis, osthelderi, geron* and *doris)*, which are mainly distributed in the eremic parts of the southern Palaearctic region, have been extensively dealt with in a previous paper (De Jong, 1974) and there is no need to repeat that treatment here. This is, however, a good opportunity to present photos of the species and to give the following corrections and additions.

Spialia phlomidis (Herrich-Schäffer)

Since my 1974 paper I could examine 90 additional specimens. They were mainly taken within the boundaries of the known distribution area, but two specimens greatly enlarged our knowledge of the distribution of this species, as they were taken in S. Iran and C. Asia, respectively. The additional localities are:

ssp. *phlomidis* (Herrich-Schäffer):
Bulgaria: Stanimaka (ZSM),
Greece: Kastoria, Mt. Chelmos, Zachlorou (near Kalavryta) (Christensen, LNK, ML, ZSM),
Turkey: Aksehir, Bulu, Cilician Taurus, Konia (LNK, ZSM),
South Russia: Eriwan (= Yerevan) (ZSM),
Iran: Golhak (near Teheran), Qader Abad Pass (Fars) (LNK, ML);
Central Asia: Alai Mts (ZSM).

ssp. *hermona* Evans:
Lebanon: Djezin (ZSM).

Spialia osthelderi (Pfeiffer)

Although the number of additional specimens examined is scarcely less than the number of specimens examined for my 1974 paper, only three localities of ssp. *gecko* can be added, all in Turkmenia: Askhabad, Merw (both ZSM) and Kara Kala (Kopet Dagh) (ML). These additions scarcely enlarge the known distribution area.

Spialia geron (Watson)

The known range of ssp. *struvei* is much extended by the capture of some specimens in E. Afghanistan, south of Safed Koh (4 ♂, 2 ♀, LNK). The male genitalia are typical of this subspecies, as are the fore wing lengths (♂ 13.5 — 14.2 mm, ♀ 14.2 — 14.3 mm). Wing length can, however, not be taken as a reliable character: smaller specimens of ssp. *struvei* do occur, as shown by two males from Dscharkent (Ili region) (ZSM), which measure 12.0 and 12.8 mm, respectively. These specimens differ further in having a dull greenish instead of yellowish underside of the hind wing. Their genitalia are of the usual *struvei* type. It is possible that on the whole the ground colour of the underside of the hind wing is more greenish in Central Asian specimens and more yellowish in Afghan specimens of ssp. *struvei,* but the material for comparison is too scanty to allow a definite statement.

The occurrence of ssp. *struvei* in Afghanistan makes it possible that the taxa known as ssp. *geron* and ssp. *struvei* are partly sympatric, as ssp. *geron* is known to occur at Arbarp (10 miles W of Kabul) (De Jong, 1974). A female from Tshehaltan (vicinity of Kabul; CN) measures 13.5 mm. For that reason it may belong to ssp. *geron,* but it can also be a small specimen of ssp. *struvei.* Unfortunately, I have not yet found characters to distinguish between ssp. *geron* and ssp. *struvei* in the female genitalia.

As the distance between the known populations of ssp. *struvei* and ssp. *geron* in Afghanistan is about 70 km, the sympatry of both forms cannot be said to be established at the moment and therefore they will provisionally be considered conspecific.

Also the range of ssp. *geron* is considerably more extensive than previously thought. In Coll. Brandt (NRS), 14 ♂ and 1 ♀ from Iran were arranged under *"osthelderi"*. The series turned out to consist of 5 ♂ of *S. osthelderi,* 4 ♂ and 1 ♀ of *S. doris,* and 5 ♂ of *S. geron.* Examination of the genitalia showed the *geron* specimens to belong to ssp. *geron.* The specimens originate from the following localities:

Iran: Fars, Shiraz, ca. 1600 m; Fars, road Shiraz—Kazeroun, Fort Sine—Sefid, ca. 2200 m; Balouchistan, Bender Tchahbahar (= Chah Bahar).

The fine spinules at the distal edge of the area spinulosa of the female genitalia in *S. geron* (cf. De Jong, 1974, fig. 11) is found in both subspecies. They seem to be absent from the edge in the other species of the *phlomidis* group and may help to distinguish *S. geron* from the very similar *S. osthelderi.*

Spialia doris (Walker)

Ssp. *doris.* On re-examination the only specimen from Kenya mentioned in my 1974 paper turned out to belong to *Spialia mafa.* Nevertheless, ssp. *doris* does occur in Kenya, according to a male caught in the semidesert area of the Northeastern Province along the Tana River between Garissa and Bura (AMNH). Further new localities of this subspecies are: El Ryadh (Saudi Arabia) (ZMB, ZSM), and the Mudugh region (Garoe, Galkayu) in Somalia (MN).

Dr. Nakamura (Williamsville, U.S.A.) kindly informed me that *S. doris* spreads northward through Israel at least as far as Herzelia, north of Tel Aviv, along the coastal sand dunes, while it also occurs in the central and northern parts of the Negev Desert. Besides *Convolvulus lanatus,* the species feeds on at least two or three more species of *Convolvulus* in Israel. The Israeli population is remarkably variable. I agree with Dr. Nakamura, that this may be due to the fact that ssp. *doris* and ssp. *amenophis* are largely intergrading in this area.

Another zone of intergradation between the last named subspecies may be found in North Sudan: a male and female from Ed Damer (Hudeiba; ZSM) are rather pale above and below, with large white markings, though not as large as usual in ssp. *amenophis*.

Ssp. *evanida*. The following two localities, both situated in the Prov. of Fars, S. Iran, can be added: Shiraz, Tchouroum (road Kazeroun—Bouchir) (NRS).

d. The *colotes* group

External characters. — Fore wing upperside with basal cell spot; central cell spot midway between basal cell spot and discocellular spot; no spots in spaces 9 and 10; submarginal spots well-developed. Median spots on underside of hind wing all present, separated or forming a continuous band, which is directed towards the dorsum; submarginal spots 4 and 5 out of line, about halfway median spots 4—5 and termen. Male with inconspicuous costal fold.

Male genitalia. — Uncus undivided; junction with tegumen slightly marked, no fenestrula. Gnathos dorsally joined to tegumen over short distance, ventrally passing into the membranous fultura superior, which is finely spinulose and folded lengthwise. Anellus with dorsal sclerotization. Aedeagus straight, surface smooth. Saccus well-developed, but shorter than uncus. Costa of valva of rather even width; costal process more or less ovoid, with spines in its ventral part, most spines pointing dorso-cephalad, but a smaller number of longer spines directed dorso-caudad. Cucullus well-developed, with a fold that partly conceals the costal process. A large, spinulose area in the membrane between costa and sacculus, joined to the costa.

Female genitalia. — Segment 8 with two dorsal and two ventral sclerites. Laterally, the dorsal and ventral sclerites almost fused, the ventral sclerites showing some small ridges at this place. Membranous postvaginal region with a slight, rather triangular sclerotization, imperceptibly passing into the deeply indented area spinulosa, which may be devoid of spines. Wall of ductus corrugated shortly before bursa, but without distinct sclerotization. No signum. Papilla analis slightly longer than broad, without basal lobe; apophysis posterior short, about as long as papilla.

Spialia colotes (Druce)

Pyrgus colotes Druce, 1875. — Proc. zool. Soc. London 1875: 416 (Angola). For synonymy, see subspecies.

External characters (pl. 2 figs. 13, 14). — This species is distinguished from all other *Spialia* species, except *confusa,* by the submarginal spots 4 and 5 of the hind wing not being in line with the other submarginal spots, but placed halfway between the median spots 4—5 and the termen. From *confusa* it can be separated by the median spots on the upperside of the hind wing being separated by the ground colour along the veins and placed more irregularly. The same difference is found on the underside of the hind wing, but in one subspecies of *colotes* the median spots are fused into a band, thus suggesting *confusa*. This band, however, has irregular sides, especially in spaces 2, 3 and 6, while it is straighter and with almost straight sides in *confusa*.

Male genitalia (figs. 44, 45). — Distal end of costa of valva rounded, not folding over costal process.

Female genitalia (figs. 47, 48). — Ventral sclerites of eighth abdominal segment touching antevaginally, but not fused. Distal rim of postvaginal area with minute spines (area spinulosa).

Ecology. — This species is mainly met with in dry, more or less wooded savanna, but I also took it in Kenya in a grassy glade in the Karura Forest near Nairobi. In Aden it has only been found above 2000 m, but in Africa it is usually found at lower altitudes.

In S. Africa *colotes* is on the wing from January to May (Swanepoel, 1953), but from localities further north I have seen specimens taken in all months, except June and July.

No food plants have so far been recorded.

Distribution (Map 6). — From Transvaal north to Angola, Ethiopia and Aden. Judging from the few localities known of this widespread species, it is a local species that possibly has been overlooked in large areas. The only country from where a reasonable number of localities are known, is Kenya.

Geographic variation. — The study of the geographic variation is hampered by the lack of material from large areas and the unequal representation from different regions, but according to the material available the following division can be made.

Spialia colotes colotes (Druce)

Pyrgus colotes Druce, 1875. — Proc. zool. Soc. Londen 1875: 416 (Angola). Holotype (♂) in the British Museum (Nat. Hist.), London.

Pyrgus nora Plötz, 1884. — Mitt. naturw. Ver. Neu-Vorpomm. 15 : 7 (Loango, Angola). Type lost. The unpublished coloured figure by Plötz was copied by Swinhoe (1908). It clearly represents the species described by Druce as *Pyrgus colotes*, as stated correctly by Swinhoe.

External characters. — Spots relatively small and widely separated; of the median spots on the upperside of the hind wing only spots 1c, 2 and 4—5 present. According to Higgins (1924), the ground colour of the upperside is rather paler brown than in ssp. *transvaaliae*, but I did not observe this difference. As large as ssp. *transvaaliae*, 9.6—11.7 mm.

A good figure of this subspecies is given by Oberthür (1912, fig. 1326).

Distribution. — Only known from Angola. Higgins (1924) mentioned this subspecies from Mombasa (Kenya). This record supposedly refers to an intermediate between ssp. *transvaaliae* and ssp. *semiconfluens*.

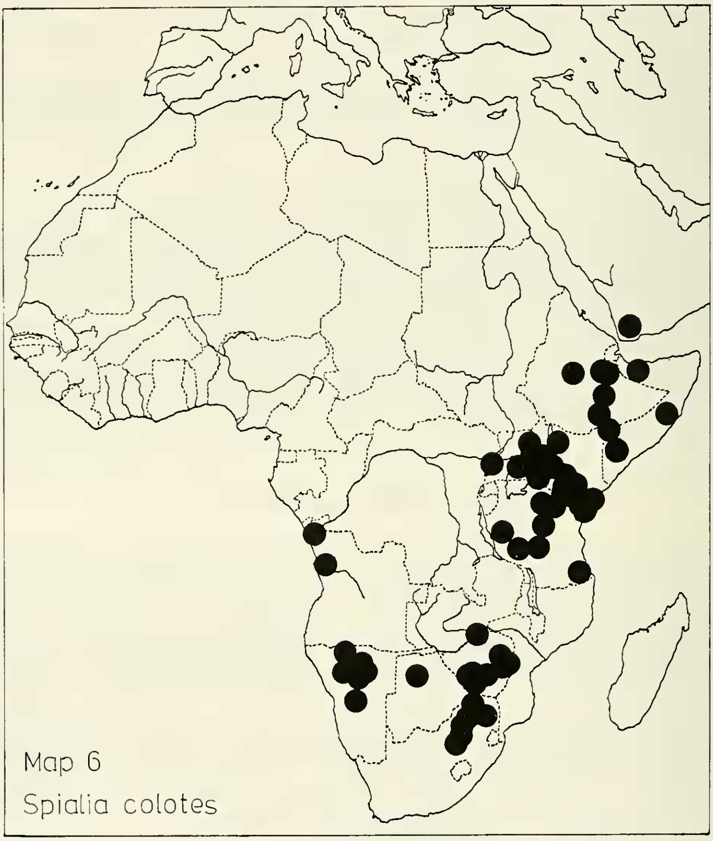
Localities. — Angola: Loango (Plötz, 1884; as *nora*); Barraca, Cuanza River (BM).

Material examined. — 6 ♂ (1 ♂ holotype), 1 ♀ , Angola (BM).

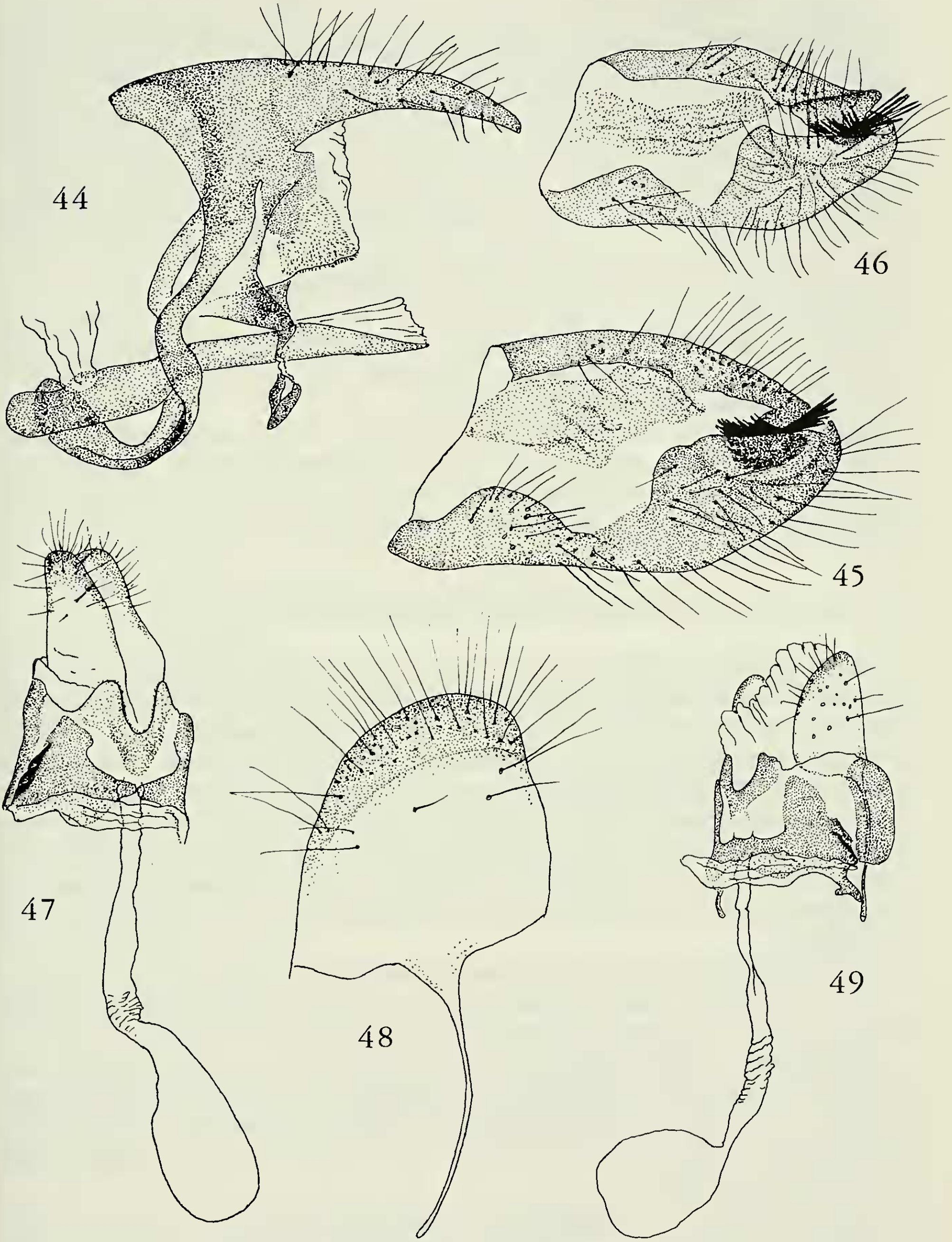
Spialia colotes transvaaliae (Trimen)

Pyrgus transvaaliae Trimen, 1889. — South African Butterflies 3: 286 (Transvaal). Holotype (♂) in the British Museum (Nat. Hist.), London.

External characters. — Spots large and prominent; on the upperside of the fore wing the inner median spots 1b and 1c fused into a single spot that is often the largest spot of the fore wing; on the upperside of the hind wing the median spots 1c, 2, 3 (usually), 4—5 and 6 present. On the underside of the hind wing the spots large, but well separated by the veins. ♂ 9.6—11.9 mm.



Distribution. — From Transvaal to Kenya and Uganda. In Kenya ssp. *transvaaliae* mainly inhabits the western and mountainous regions. In the drier eastern and southern parts it is replaced by ssp. *semiconfluens*, but many intermediate specimens can be found. In Uganda ssp. *transvaaliae* occurs in the wetter areas; in the dry northeastern part it encounters ssp. *semiconfluens*. Apparently intermediate populations are listed after ssp. *semiconfluens*, but intermediate specimens can also be found in other localities.



Figs. 44—46. Male genitalia, lateral aspect, and inside of right valva. 44—45, *S. colotes transvaaliae* (Sigor, Kenya). 46, *S. confusa obscura* (Arabuko forest, Kenya). Figs. 47—49. Female genitalia, latero-ventral aspect, and papilla analis. 47—48, *S. colotes transvaaliae* (Arusha, Tanzania). 49, *S. confusa confusa* (Upper Luangwa Valley, Zambia).

Localities. — Kenya: Lake Baringo, Bura (Teita), Chawia Forest (Teita Hills), Chepalungu, Chyulu Hills, Mt. Elgon, Escarpement, Fourteen Falls, Gilgil, Karen, Karura Forest, Davirondo, Kima, Kisii, Kisumu, Kitui, Langata, Lumbwa, Mekueni, Maranga, Meru, Mombasa, Nairobi, Ngong, Shimba Hills, Sigor, Sultan Hamud, Teita Hills (AMNH, BM, CMP, ML, MN, NRS, USNM). Uganda: Bukedi, Bundibugyo, Jinja (AMNH, ML, NMB). Tanzania: Arusha Nat. Park, Chimala River, Great Craters, 60 mls S of Kondoa Irangi, Mt. Meru, Mkoe, Mpanda, Ruaha Nat. Park (BM, ML, MN, ZSM). Rhodesia: Chirundi, Dotts Drift, Filabusi, Gwanda, Matetsi, Matopos, Nyanadzi River, Odzi River, Rusape, Sabi Valley, West Nicholson (MN, NMB). South Africa. Transvaal: Blaauwberg, Dendron, Johannesburg, De Kroon, Leydsdorp, Pietersburg, Potchefstroom, Potgietersrust, Tubex, Vivo, Warmbaths (BM; Swanepoel, 1953). Botswana: Maun, 16 mls N of Maun (NMB). Namibia: Grootfontein, Grünfelde, Kalidona, Okahandja, Otjitambi, Tsumele, Waterberg, Windhoek (SMW, ZSM).

Material examined. — 124 ♂ , 47 ♀ : 99 ♂ , 29 ♀ , Kenya (AMNH, BM, CMP, ML, MN, NRS, USNM); 3 ♂ , Uganda (AMNH, ML); 7 ♂ , 3 ♀ , Tanzania

Material examined. — 124 ♂ , 47 ♀ : 99 ♂ , 29 ♀ , Kenya (AMNH, BM, CMP); 10 ♂ , 12 ♀ , Namibia (BM, SMW, ZSM).

Spialia colotes semiconfluens subspec. nov.

External characters (pl. 2 figs. 13, 14). — On the upperside the spots are smaller than in ssp. *transvaaliae*, particularly the inner median spots 1b and 1c of the fore wing and the median spot 1c of the hind wing, but contrary to ssp. *colotes*, all spots of ssp. *transvaaliae* are present. On the underside of the hind wing the median spots are also smaller than in ssp. *transvaaliae*, but they are fused into a continuous band, usually with the exception of median spot 7 which is separated by dark scaling on vein 7. By the continuous band this subspecies is suggestive of *Spialia confusa*, but in that species the band is much more regularly shaped and the median spots are also fused into a continuous band on the upperside of the hind wing.

Ssp. *semiconfluens* is on the average slightly smaller than the other subspecies: ♂ 9.3—10.9 mm. In most specimens the ground colour of the upperside is rather paler brown than in ssp. *transvaaliae*.

Distribution. — Aden, Ethiopia and Somalia and southwards into Kenya and Uganda. In Kenya this subspecies flies especially in the dry east and southeast and is replaced by ssp. *transvaaliae* in the less dry mountainous regions and western part of the country. In Uganda ssp. *semiconfluens* is restricted to the dry north-eastern regions.

Material examined. — Holotype: ♂ , Bihendula (Somalia), 4.xi.1949, K. M. Guichard. Paratypes: 1 ♂ , Bihendula (Somalia), 1 v. 1949, K. M. Guichard; 1 ♂ , Harar (Ethiopia), 23.xi.1939, R. E. Ellison; 1 ♂ , W. Errer Valley (Ethiopia), 28.xi.1939, R. E. Ellison; 1 ♂ , E of Errer Valley (Ethiopia), 19.xi.1939, R. E. Ellison; 1 ♀ , Fich Shoa Prov. (Ethiopia), 8.v.1947, K. M. Guichard. All types in the British Museum (Nat. Hist.), London.

Further material. — 49 ♂, 20 ♀ : 3 ♂, 1 ♀, Somalia (Bardera, Bihendula, GanLibah, Haro-Bussar) (BM); 11 ♂, 5 ♀, Ethiopia (Dakotta Valley, Dire Dawa, Errer Valley, Fich, Harar, Mulata Mts) (AMNH, BM); 1 ♂, 2 ♀, South Yemen (Jebel Jihaf) (BM); 23 ♂, 10 ♀, Kenya (Kacheleba, Kenani, Kima, Kitui, Kulal, Makueni, Mutomo, Namanga, Ukazzi Hill (AMNH, MN); 11 ♂, 2 ♀, Uganda (Amudat, Kotido) (MN).

Material examined from populations intermediate between ssp. *transvaaliae* and ssp. *semiconfluens*. — 22 ♂, 4 ♀, Kenya (Besil, Kibwezi, Voi) (BM, ML).

Spialia confusa (Higgins)

Hesperia transvaaliae var. *confusa* Higgins, 1924. — Trans. ent. Soc. London 1924: 90 (SW shore Lake Nyassa). For synonymy, see subspecies.

External characters (pl. 2 figs. 15, 16). — Readily distinguished from all other *Spialia* species except *colotes* by the basad shift of the submarginal spots 4 and 5 of the hind wing. From *colotes* it can be separated by the median spots of the hind wing, which are fused into a continuous band, not only on the underside, but also on the upperside. The band on the underside of the hind wing is much more regularly shaped than in *colotes semiconfluens*. In rare doubtful cases the genitalia have to be checked for identification.

Male genitalia (fig. 46). — Distal end of costa of valva slightly protruding and folding over costal process.

Female genitalia (fig. 49). — Ventral sclerites of eighth abdominal segment broadly fused antevaginally. Sclerotization in postvaginal area slightly stronger than in *colotes*, without spines along distal edge.

Ecology. — Very little is known about this apparently rare species. Swanepoel (1953) found it in Natal "playing along a road that leads through the bush", and I took it along very dry, sandy roads in the Arabuko Forest near Malindi, Kenya. It is difficult to capture as it is a small and swift species, which frequently skips from sun-lit places into shadows and then appears to be lost.

It may be on the wing throughout the year, but I have not seen specimens or records from May and June.

According to Sevastopulo (1974) the larvae live on *Melhamia* (Sterculiaceae) and *Triumfetta* (Tiliaceae).

Distribution (Map 7). — This species has been observed over a wide range, from Natal to Kenya, in seven countries, but at relatively few localities.

Geographic variation. — There is some variation in the development of the spots, but in view of the scarce material any division into subspecies can only be provisional.

Spialia confusa obscura (Higgins)

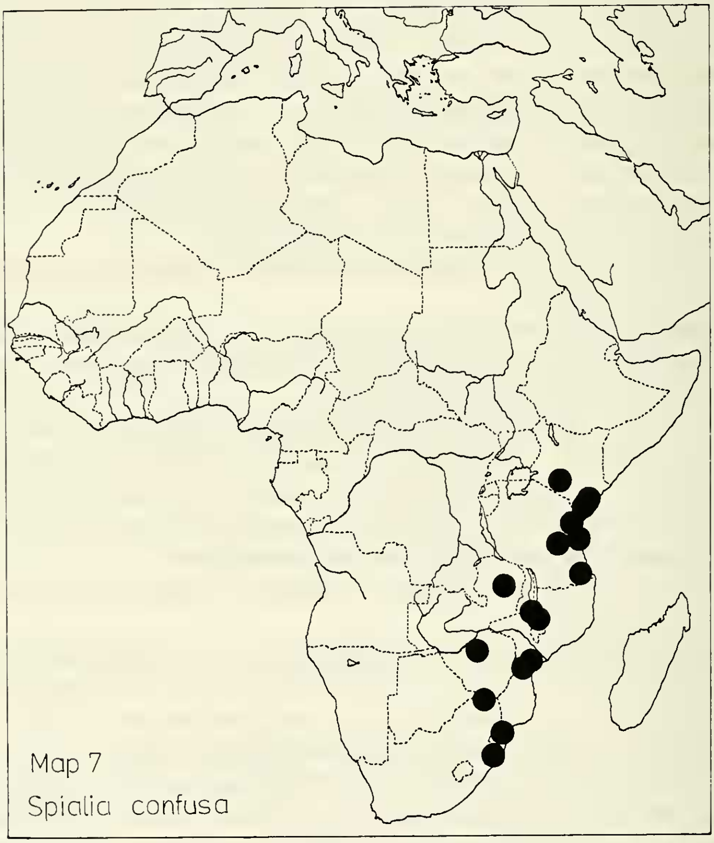
Hesperia transvaaliae var. *obscura* Higgins, 1924. — Trans. ent. Soc. London 1924 : 92—93 (Nairobi). Holotype (♂) in the British Museum (Nat. Hist.), London.

External characters (pl. 2 figs. 15, 16). — A dark form, with smaller spots. On the upperside of the fore wing the central cell spot vestigial or absent, on the upperside of the hind wing median spot 1c faint or absent. ♂ 8—10.2 mm.

Distribution. — The northern part of the range of the species, in Kenya and N. Tanzania.

Localities. — Kenya: Arabuko Forest, Nairobi, Rabai, Sokoke Forest, Shimba Hills (AMNH, BM, ML, MN; Sevastopulo, 1974). Van Someren (1939) mentioned *confusa* in a report on his expedition to the Chyulu Hills, but his specimens (in MN) turned out to belong to *S. colotes transvaaliae* with slight influence of ssp. *semiconfluens*. Tanzania: Amani, Dar-es-Salaam, Paga Hill (BM, MN).

Material examined. — 17 ♂, 3 ♀ : 14 ♂ (1 ♂ holotype), 2 ♀, Kenya (AMNH, BM, ML, MN); 3 ♂, 1 ♀, Tanzania (BM, MN).



Spialia confusa confusa (Higgins)

Hesperia transvaaliae var. *confusa* Higgins, 1924. — Trans. ent. Soc. London 1924 : 90 (SW shore Lake Nyasa, between Ft. Johnston and Monkey Bay). Holotype (♂) in the British Museum (Nat. Hist.), London.

Hesperia transvaaliae var. *fasciata* Higgins, 1924. — Trans. ent. Soc. London 1924 : 90—91 (between Ft. Mangoche and Chikala Boma, Malawi). Holotype (♀) in the British Museum (Nat. Hist.), London. Evans (1937) incorrectly stated the type to be a male.

External characters. — Spots larger than in the foregoing subspecies; on the upperside of the hind wing median spot 1c well-developed. ♂ 9.8—10.9 mm.

The type of *fasciata* is not clearly different from that of *confusa,* except for the median band on the hind wing, which is rather narrower. There is no apparent reason to rank *fasciata* otherwise than as a forma of ssp. *confusa.*

Distribution. — The southern part of the range of the species, from C. Tanzania and N. Zambia to Natal.

Localities. — Tanzania: Mikumi Nat. Park, Mkami, Mkoe (ML, ZSM). Zambia: Upper Luangwa Valley, Petauke (BM, HDE; Neave, 1910, as *"Hesperia bettoni"*). Malawi: between Ft. Johnston and Monkey Bay, between Ft. Mangoche and Chikala Boma (BM). Rhodesia: Sanyati Valley (= Umniati R.) (NMB). Mozambique: Delagoa Bay, Inhaminga, Siluve (= Xiluvo) Hills (BM, NMB, USNM, ZSM). South Africa. Natal: False Bay, Hluwehluwe, Messina, Zulu (NMB, NRS; Swanepoel, 1953).

Material examined. — 18 ♂ , 5 ♀ : 3 ♂ , 1 ♀ , Tanzania (ML, ZSM); 2 ♂ , 1 ♀ , Malawi (1 ♂ holotype *confusa,* 1 ♀ holotype *fasciata*) (BM); 5 ♂ , 3 ♀ , Zambia (BM, HDE); 6 ♂ , Mozambique (BM, USNM, ZSM); 1 ♂ , South Africa (NRS).

e. The *sertorius* group

External characters. — Fore wing with or without basal cell spot on upperside; if basal cell spot present, then central cell spot about midway between basal cell spot and discocellular spot or slightly closer to basal cell spot; no spots in spaces 9 and 10; submarginal spots usually all present, but may be vague. Median spots on underside of hind wing form a continuous band or spot 6 is absent; submarginal spots 4 and 5 in line with the other submarginal spots. Male without costal fold.

Male genitalia. — Uncus undivided; at junction with tegumen in some species with large fenestrula. Gnathos dorsally not fused to tegumen, well sclerotized, ventrally forming enlarged and spined "heads"; left and right part of gnathos ventrally united by a usually smooth membrane. Anellus membranous. Aedeagus more or less straight, surface smooth. Saccus relatively short, shorter than uncus. Costa of valva narrow; costal process well developed, more or less oval, ventrally with spines which are directed dorso-distad. Cucullus dorsally excavated or with a small fold that partly overlaps the costal process. A hairy fold in the membrane between costa and cucullus.

Female genitalia. — Segment 8 with two dorsal sclerites, medially separated by a membrane, and two ventral sclerites, united antevaginally by a narrow sclerotization. Dorsal and ventral sclerites more or less fused. Postvaginally a membranous region with a proximally narrow, distally broadening sclerite, which at the distal edge of the segment passes into the spinoluse region, or without this sclerite so that the area spinulosa can be seen as a dark patch in the membranous distal part of the ventral surface. Ductus gradually broadening into bursa. Ductus and bursa without ornamentation, or bursa with a finely spinulose area. Papilla analis with basal lobe; apophysis posterior long, longer than papilla.

Superspecies *Spialia mafa*

External characters. — Fore wing with a basal cell spot on the upperside. Median spots on the underside of the hind wing complete or spot 6 is absent.

Male genitalia. — A large fenestrula at the junction of uncus and tegumen. Heads of gnathos larger than in superspecies *Spialia sertorius*. Costa of valva continued beyond the costal process as a finger-shaped projection. Hairy fold at the inside of the valva obvious, oblique, wavy or branched.

Female genitalia. — Dorsal sclerites of eighth abdominal segment fused to the ventral sclerites along the proximal edge of the segment, leaving a wide membranous area, or connecting sclerotization between dorsal and ventral sclerites more extensive, enclosing a membranous area. Bursa copulatrix with or without ornamentation.

Ecology. — Food plants: Malvaceae.

Distribution. — Very widely distributed, from South Africa through East Africa, Saudi-Arabia and India to Hainan. It replaces the superspecies *Spialia sertorius* in the Old World Tropics.

Spialia mafa (Trimen)

Pyrgus mafa Trimen, 1870. — Trans. ent. Soc. London 1970 : 386, pl. 6 fig. 12 (Maseru, Basutoland). For synonymy, see under subspecies.

External characters (pl. 4 figs. 25, 26). — From the other species of the *sertorius* group, *mafa* is easily distinguished by the combination of the presence of a basal cell spot on the upperside of the fore wing and the absence of median spot 6 on the underside of the hind wing. The other *Spialia* species, which almost or entirely lack median spot 6 on the underside of the hind wing and occur in the Ethiopian region, are *doris, paula* and *spio*. The differences with these species have been outlined in the key and it is unnecessary to repeat them here.

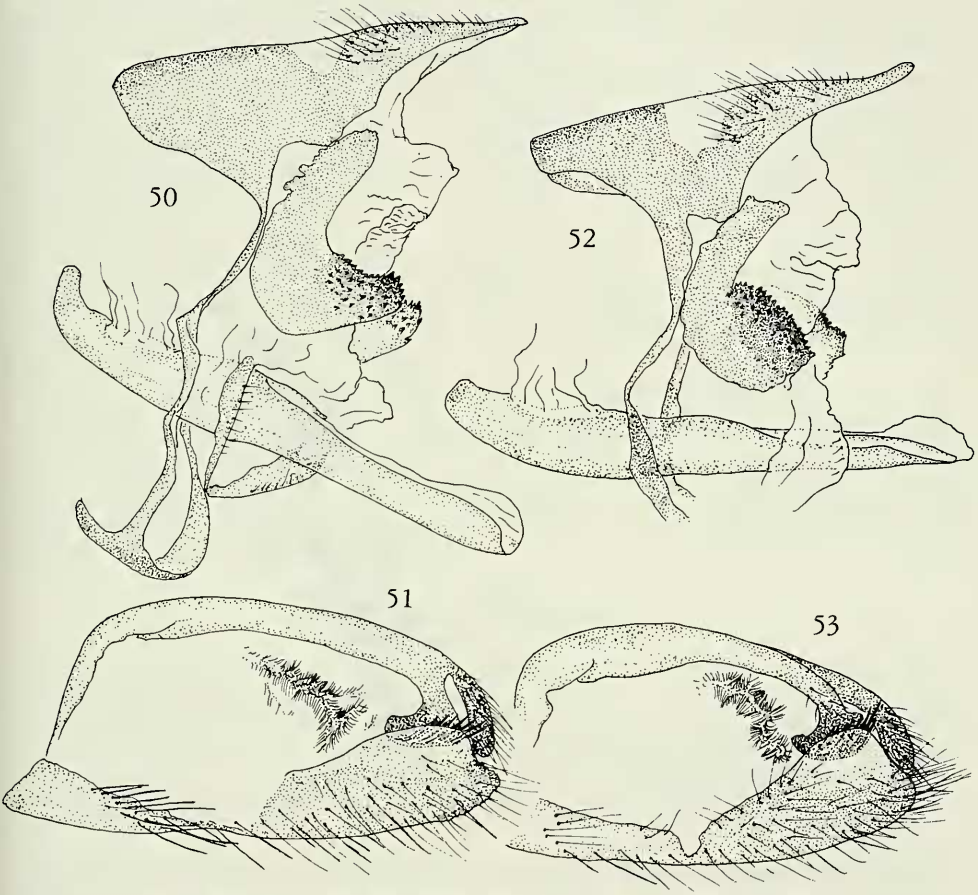
There is some variation in the extension of the spots. On the upperside of the hind wing the median spots 1c—5 are usually present, 6 is always absent. The ground colour of the underside of the hind wing is lighter or darker yellowish or brownish.

See further under Geographic variation.

Male genitalia (figs. 50, 51). — At junction of uncus and tegumen a large fenestrula. Spined heads of gnathos rather slender, less than half of entire gnathos. Costal process of valva situated before distal end of costa. Distal part of costa looks like a finger-shaped projection of the costa instead of being the costa itself. Cucullus with short fold covering ventral part of costal process. On the inside of the valva, between costa and cucullus, a large, branched fold, very thickly beset with short hairs.

Female genitalia (figs. 54, 55). — Dorsal sclerites of segment 8 more or less fused with ventral sclerites, enclosing a small, membranous area. Ventral sclerites antevaginally conjoined by a narrow sclerotization, postvaginally separated by a narrow membranous strip. This strip widens distally and passes into the non-sclerotized area spinulosa, which has a more or less straight distal edge. Bursa without ornamentation. Papilla analis rather narrow, apex rounded.

Ecology. — Like most other *Spialia* species, *mafa* prefers more or less open country, but judging from its distribution it largely avoids low-lying areas, being mainly found in hilly or mountainous regions. In Kenya I took this species in open places in a more or less wooded area up to 2000 m (between Nanyuki and Naro Moru) and Gabriel (1954) recorded specimens from Yemen captured up to more than 2500 m. According to Swanepoel (1953) it is a scarce and local species, at least in South Africa.



Figs. 50—53. Male genitalia, lateral aspect, and inside of right valva. 50—51, *S. mafa higginsi* (Kenya). 52—53, *S. galba galba* (Ceylon).

In appropriate places *mafa* may be on the wing throughout the year, but in many areas adults are absent or very scarce in June, July and August.

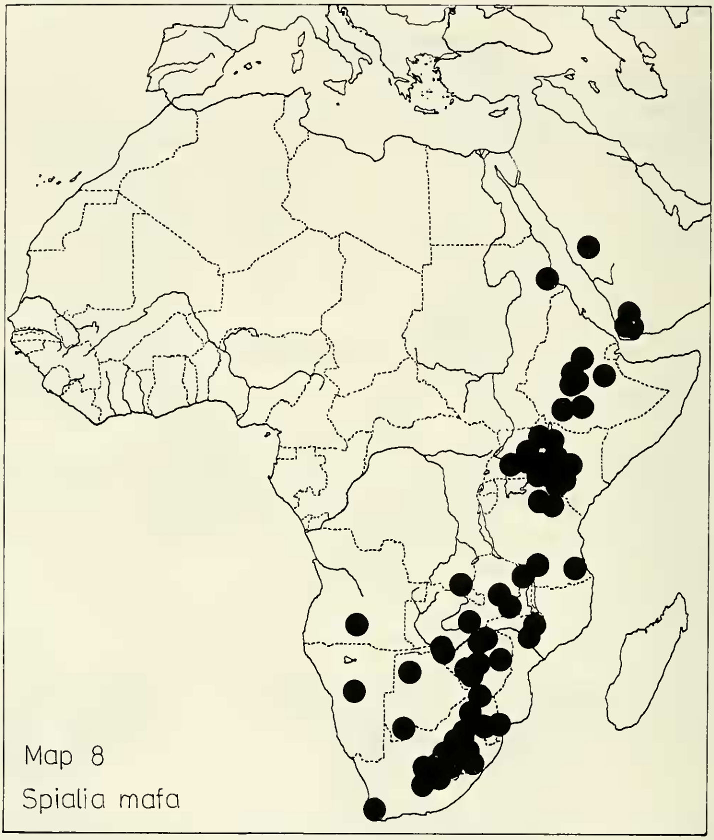
The only recorded food plant is *Hibiscus aethiopicus* L. (Malvaceae) (Murray, 1959).

Distribution (Map 8). — South and East Africa, not known from Angola, and Zaïre except for the extreme south. Distributed from Cape Town and SW Africa to Ethiopia and Sudan, and extending into the Arab peninsula, where it occurs as far east as Oman.

Geographic variation. — There is a marked geographic variation in the size of the specimens and the development of the spots. Two subspecies are distinguished.

Spialia mafa higginsi Evans

Spalia mafa higginsi Evans, 1937. — Catal. Afric. Hesp. : 62 (Mumias, Kenya). Holotype (♂) in the British Museum (Nat. Hist.), London.



External characters (pl. 4 figs. 25, 26). — The original description reads: "Below, the markings are broader and on the hind wing the basal spot in space 7 and the discal spot in space 1c are not detached as in *mafa*". These differences are rather slight, but more conspicuous differences can be found in the following characters:

1. ssp. *higginsi* is smaller than ssp. *mafa*, ♂ (8.5—) 9.2—10.7 (—11.3) mm, ♀ 9.8—11.3 (—12.6) mm, as against ssp. *mafa* ♂ 9.9—11.7 mm, (9.1—) 10.2—12.5 mm. This difference is conspicuous if one can compare long series of both subspecies;
2. in ssp. *mafa* the median spot 5 on the underside of the hind wing is almost always extended basad, just above the continuation of vein 5 in the cell; this is almost never, and certainly never conspicuously the case in ssp. *higginsi*.

Distribution. — The northern part of the range of the species. The southern limit presumably runs through Malawi, Zambia and S. Zaïre. As most specimens examined from Zambia show characters of ssp. *mafa,* all specimens from this country have provisionally been listed under that subspecies. Additional material will possibly indicate a transition zone. The specimens examined from S. Zaïre are listed under the present subspecies, but they probably also belong to the transition zone.

Localities. — Saudi-Arabia: Ashaira (BM). Oman: Khasab, Nizwa area, Rostaq (Larsen, 1977). Yemen: Hada, San'a, Suq-es-Sabt (N of Ibb) (BM, ZSM; Gabriel, 1954). South Yemen: Dhala, Jebel Jihaf (BM; Gabriel, 1954). Sudan: Erkowit (Prov. Kassala) (ZSM). Ethiopia: Addis Abeba, Burdji, Daroli, Dessiè, Getri, Harar, Jowaha, Negelli, Ft. Zuguala (BM, MN, ZSM). Kenya: Besil (= Bissil), Broderick Falls, Bura (Teita), Campi-ya-Moto, Escarpment, Gilgil, Ilala, Kabarnet, Kedai, Kima, Kitale, Mazoe Valley, Meru Distr., Migori Valley, Mirua Valley, Mt. Kenya, Muruanysigar Mt. (Turkana), Nairobi, Naro Moru, Ngong Escarpment, Olkasale, Rumuruti, Saboti Hill, Soi, Stony Athi, Subukia, Thomson Falls (AMNH, BM, ML, MN, MNHN, USNM). Uganda: Entebbe, Koki Country, Siroko River, Tororo, Queen Elisabeth Park (AMNH, BM, CMP, MN). Tanzania: Chukwe (Mpanda), District of Great Craters, Njombe, Tendaguru (BM, ML). Zaïre: Kapiri, Musonoie (BM, MRAC). Malawi: Cholo (CMP).

Material examined. — 104 ♂, 44 ♀ : 1 ♂ Saudi-Arabia (BM); 7 ♂, 2 ♀, Yemen (MB, ZSM); 4 ♂, 4 ♀, South Yemen (BM); 2 ♂, Sudan (ZSM); 11 ♂, 3 ♀, Ethiopia (BM, MN, ZSM); 64 ♂ (1 ♂ holotype of *higginsi*), 29 ♀, Kenya (AMNH, BM, ML, MN, USNM); 8 ♂, 6 ♀, Uganda (AMNH, BM, CMP, MN); 4 ♂, Tanzania (BM, ML); 2 ♂, Zaïre (BM, MRAC); 1 ♂, Malawi (CMP).

Spialia mafa mafa (Trimen)

Pyrgus mafa Trimen, 1870. — Trans. ent. Soc. London 1870 : 386, pl. 6 fig. 12 (Maseru, Basutoland). Holotype (♂) in the British Museum (Nat. Hist.), London.

Hesperia oberthüri Aurivillius, 1925. — In: Seitz, Macrolepidoptera of the World 13 : 565 (Kimberley). Holotype (♀) in the British Museum (Nat. Hist.), London. This name was given to a figure of *mafa* by Oberthür, which was incorrectly named *transvaaliae.* The figured specimen is in the BM. Preoccupied by *Hesperia oberthüri* Leech, 1891 (now placed in the genus *Pyrgus*).

Pyrgus aurivillii Shepard, 1935. — Lepid. Catalogus, Pars 69 : 496. Replacement for *Hesperia oberthüri* Aurivillius.

External characters. — The differences with ssp. *higginsi* have been dealt with under that subspecies.

Distribution. — The southern part of the range of the species, from S. Zaïre, Zambia and Malawi southwards.

Localities. — Zambia: Chilanga, Fort Jamieson, Livingstone, Luangwa Valley (BM, MN; Neave, 1910). Malawi: Florence Bay, Ruo Valley (BM; Gifford, 1965). Rhodesia: Bulawayo, Darwendale, Essexvale, Hope Fountain, Matetsi, Matope Hills, Odzi, Salisbury, Selukwe, Umtali, X-mas Pass (BM, CMP, MN, NMB). Mozambique: Rikatla (24 km N of Lourenço Marques) (BM). Botswana: Sepopa, Tshabong (NMB). South Africa. Transvaal: Balfour, Barberton, Crocodile River, Dendron, Germiston, Haenertsburg, Johannesburg, Limpopo River, Messina, Pietersburg, Potchefstroom, Pretoria, Rustenburg, Shilouvane (BM, CMP, MN, NMB; Swanepoel, 1953; Trimen, 1870). Natal: Bergville, Estcourt, Frere, Greytown, Howick, Impenza, Ladysmith, Loesskop, Middle Rest, Montello, Muden, Newcastle, Pitzkop, Tugela River, Weenen (AMNH, BM, MN, MRAC; Swanepoel, 1953). Orange Free State: Bethulie, Bloemfontein, Ladybrand, Vaal River (AMNH, BM, MRAC, NMB; Swanepoel, 1953). Cape Province: Barkly District, Brakfontein, Burghersdorp, Cape Town, Durbansville, Katzenberg, Kimberley, Lions Head, Malmesbury, Mamre, Maseru, Melkbosch, Stellenbosch, Tijgerberg (BM, ML, MN, MNHN, MRAC, NMB; Swanepoel, 1953). Lesotho: Koro Koro, Maseru, Namanthes (BM, NMB; Swanepoel, 1953; Trimen, 1870). Namibia: Niangana, Okahandja (SMW). Angola: Ehanda (Trimen, 1891).

Material examined. — 73 ♂, 56 ♀ : 4 ♂, 1 ♀, Zambia (BM); 1 ♂, 1 ♀, Malawi (BM); 5 ♂, 1 ♀, Rhodesia (BM, CMP, MN); 1 ♂, Mozambique (BM); 62 ♂ (1 ♂ holotype *mafa*), 49 ♂, South Africa (AMNH, BM, CMP, ML, MRAC); 4 ♀, Namibia (SMW).

Spialia galba (Fabricius)

Hesperia galba Fabricius, 1793. — Entomologia Systematica 3 : 352 (Tranquebar).

External characters (pl. 4 figs. 27, 28). — From the other species of the *sertorius* group *galba* is easily distinguished by the combination of a well-marked basal cell spot on the upperside of the fore wing and an unbroken, rather regular median band on the underside of the hind wing. As *galba* is the only real Oriental species of the genus, confusion with other *Spialia* species is unlikely. However, in the extreme west of the Oriental Region distributional overlap with *zebra* and *doris* does not seem impossible and it may be convenient to mention some differences.

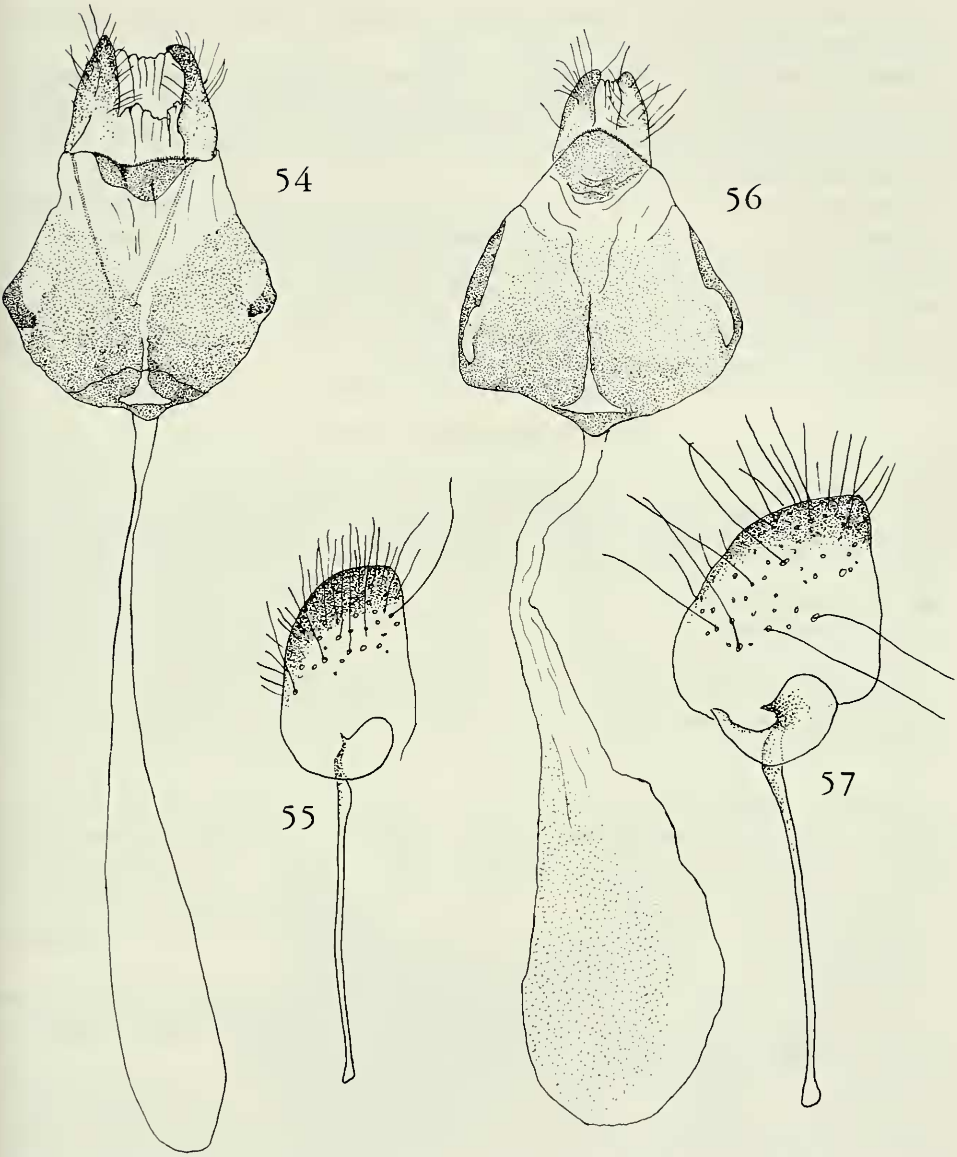
From *zebra*, *galba* is distinguished by the presence of a well-marked basal cell spot on the upperside of the fore wing, and from *doris* by the unbroken median band on the underside of the hind wing.

There is some variation in the development of the spots and in the size (♂ 9.4—11.8 mm), but the variation does not appear geographic, except for the variation mentioned under Geographic variation.

Swinhoe (1913) thought "*Pyrgus evanidus* Butler" to be "undoubtedly the extreme cold-weather form of *galba*". However, "*Pyrgus evanidus*" is considered a subspecies of *Spialia doris* (cf. De Jong, 1974).

Male genitalia (figs. 52, 53). — Very large fenestrula at junction of uncus and tegumen. Gnathos with large ventral "heads", occupying more than half of the entire gnathos. Costal process of valva placed before distal end of costa; continuation of costa finger-shaped, longer than in *mafa*. Cucullus with narrow fold, just covering ventral side of costal process. Between costa and cucullus a winding, but unbranched hairy fold on the inside of the valva.

Female genitalia (figs. 56, 57). — Dorsal sclerites of segment 8 along proximal edge fused with ventral sclerites. Ventral sclerites conjoined antevaginally by a narrow sclerotization. Postvaginally there is a triangular membranous area, distally enclosed by the ventral sclerites, which fuse while the sclerotization weakens. Distal edge of ventral sclerites vague, sclerotization passing into membrane that forms a pointed area spinulosa. Bursa with large area of small spines. Papilla analis rather



Figs. 54—57. Female genitalia, ventral aspect, and papilla analis. 54—55, *S. mafa higginsi* (Kenya). 56—57, *S. galba galba* (Ceylon).

short and broad, less rounded than in *mafa*, slightly triangular; basal lobe large, curving.

Ecology. — *S. galba* can commonly be found throughout the year in all sorts of open country, but in some areas it is absent during the dry season. It ascends to 2400 m in the Himalayas (ZSM) and to 2600 m in South India (Wynter-Blyth, 1957), but in Ceylon it is rare above 1300 m (Woodhouse, 1950).

Recorded food plants are *Sida rhombifolia, Hibiscus* and *Waltheria indica* (all Malvaceae) (Swinhoe, 1913; Woodhouse, 1950).

Distribution (Map 9). — Throughout India and Ceylon. In the west it extends to Karachi and Chitral, in the east it penetrates Burma as far as the S. Shan States. A single specimen is known from eastern Thailand. Still further east it occurs isolated in the island of Hainan.

Geographic variation. — Over its large Indian area *galba* does not seem to vary geographically, but in the east two subspecies can be distinguished, one confined to Hainan, the other occurring in Burma. It is obscure how far the Burmese subspecies comes into contact with the nominate form from India. The single known specimen from Thailand cannot be distinguished from Indian specimens, so for the time being it is listed under the nominate subspecies.

Spialia galba galba (Fabricius)

Hesperia galba Fabricius, 1793. — Entomologia Systematica 3 : 352 (Tranquebar).
According to Zimsen (1964) the type material includes three specimens. One of these specimens (which are in the Universitetets Zoologiske Museum, Copenhagen), however, though bearing a label with *"H. Galba"* in probably Fabricius' handwriting, comes from West Africa ("Guinee") and belongs to *S. diomus*. The remaining two specimens do not bear locality labels, but as they belong to the only *Spialia* species known to occur at the type locality of *S. galba*, one of these specimens comes into consideration as type specimen. One specimen, labelled *"Galba"* in probably Fabricius' handwriting, lacks the abdomen. The other specimen, a male labelled "Mus. Seh. e T.L." (i.e. "Museum Sehestedt e Tønder Lund") is best fitted for lectotype designation, as Fabricius mentioned the specimen to be in the Sehestedt collection. I have labelled the specimen accordingly.
Pyrgus superna Moore, 1865. — Proc. zool. Soc. London 1865 : 792 (Calcutta). Holotype (♀) in the British Museum (Nat. Hist.), London.

External characters (pl. 4 figs. 27, 28). — On the upperside of the fore wing median spot 4 conspicuously smaller than median spot 3, or absent; submarginal spot 2 in line with the other submarginal spots. ♂ 9.4—11.8 mm. Larger and smaller specimens occur throughout the area. A very small specimen (♂) from the Himalayas (Simla) was named ab. *minuscula* by Reverdin (1933), a redundant name; the specimen is in the ZSM.

Distribution. — The western subspecies, occupying the whole range of the species west of Burma. As the single known specimen from Thailand cannot be distinguished from this subspecies, it is provisionally listed here.

Localities. — Pakistan: Chitral, Karachi (BM, LNK). India: throughout, from Kutch in the west to the Naga Hills in the east, and from Kashmir in the north to Madras in the south (AMNH, BM, ML, ZSM). Ceylon: throughout (AMNH, BM, CMP, ML, USNM). Nepal: Baklore (W. Terai), Bhainse Dobhan (Chisapani Garhi), Katmandu, Katmandu Valley, Magarkot Manbu, Rangit Valley, Rapti Valley, Sun Khosi Valley (AMNH, BM, ZSM). Sikkim: Sikkim (BM, UNSM). Bhutan: Bhutan (BM, USNM). Thailand: Khun Kaen (USNM).

Material examined. — 229 ♂, 163 ♀ : 6 ♂, 2 ♀, Pakistan (BM, LNK); 157 ♂, 118 ♀, India (AMNH, BM, CMP, ML, ZSM); 34 ♂, 24 ♀, Ceylon (AMNH, BM, CMP, ML, USNM); 19 ♂, 10 ♀, Nepal (AMNH, BM, NRS, ZSM); 11 ♂, 8 ♀, Sikkim (BM, USNM); 2 ♂, 1 ♀, Bhutan (BM, USNM); 1 ♂, Thailand (USNM).

Spialia galba shanta Evans

Spialia galba shanta Evans, 1956. — Ann. Mag. Nat. Hist. (12) 9 : 750 (Hsipaw, S. Shan States). Holotype (♂) in the British Museum (Nat. Hist.), London.

External characters. — On the upperside of the fore wing median spot 4 well-developed, as large as median spot 3; submarginal spot 2 in line with the other submarginal spots. ♂ 10.4—11.5 mm.

Distribution. — N. and S. Shan States, Burma.

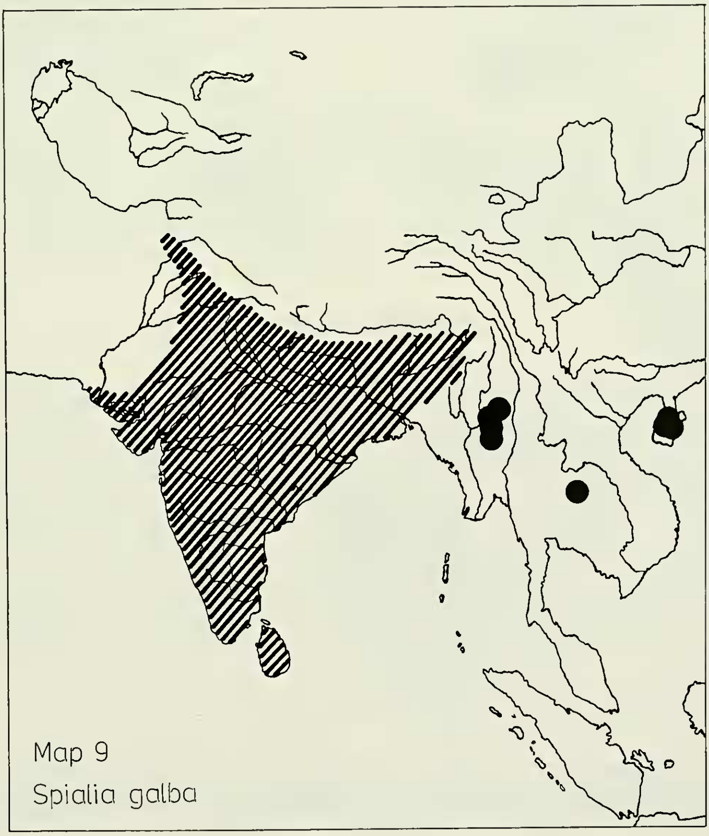
Localities. — Burma: Hsipaw, Maymyo, Tilin Yaw, Poungadaw nr. Thayetmyo, Myingyan, 40 km E. of Taunggyi (BM, NRS).

Material examined. — 7 ♂, 12 ♀, Burma (incl. ♂ holotype) (BM, NRS).

Spialia galba chenga Evans

Spialia galba chenga Evans, 1956. — Ann. Mag. Nat. Hist. (12) 9 : 750 (Kiung-Chow, Hainan). Holotype (♂) in the British Museum (Nat. Hist.), London.

External characters. — On the upperside of the fore wing median spots 3 and 4 equal, as in ssp. *shanta*, submarginal spot 2 placed further from termen than in



other subspecies, giving the submarginal series a much more sinuous aspect. ♂ 10.6—10.7 mm.

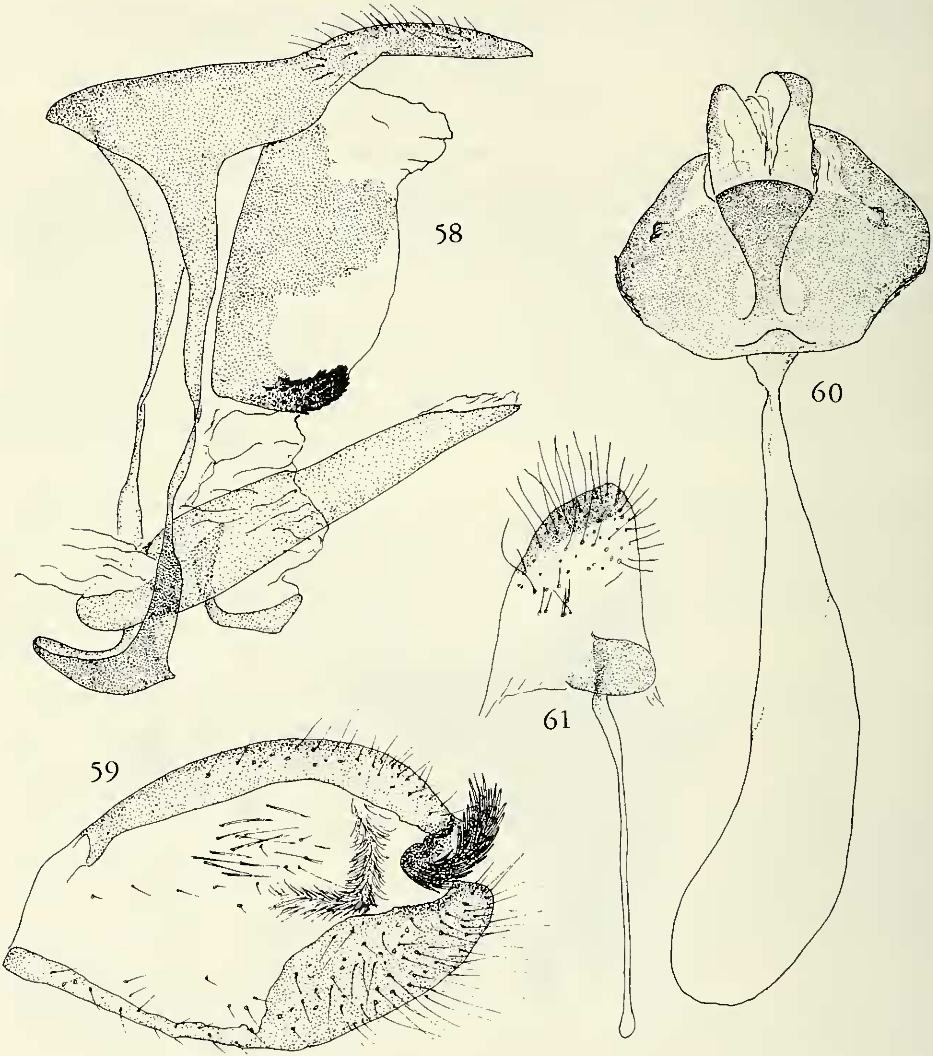
Distribution. — Hainan.

Localities. — Hainan: Cheng-Mai, Kiung-Chow, Porten, Youboi (BM).

Material examined. — 2 ♂, 3 ♀, Hainan (incl. ♂ holotype) (BM).

Superspecies *Spialia sertorius* (Hoffmansegg)

This superspecies has extensively been dealt with in my previous paper on



Figs. 58—59. Male genitalia, lateral aspect, and inside of right valva of *S. orbifer orbifer* (Greece). Figs. 60—61. Female genitalia, ventral aspect, and papilla analis of *S. sertorius sertorius* (Chiclana, S. Spain).

Spialia (De Jong, 1974). It may suffice to mention here only the characters by which the two constituting species are distinguished from other *Spialia* species and to give some new information on the distribution of the species.

External characters (pl. 4 figs. 29—32). — From the other species of the *sertorius* group, viz., *mafa* and *galba, sertorius* and *orbifer* are easily distinguished by the absence of a basal cell spot on the upperside of the fore wing, while this character in combination with the absence of median spot 6 on the underside of the hind wing and the direction of the median band towards the inner spot in space 7 separates *sertorius* and *orbifer* from all other *Spialia* species.

Male genitalia (figs. 58, 59). — No fenestrula at junction of uncus and tegumen. Gnathos with relatively narrow heads. Costal process of valva at distal end of costa. Cucullus dorsally hollowed to receive the costal process, but without definite fold. Hairy fold between costa and cucullus on inside of valva curved or angled, neither winded nor branched.

Female genitalia (figs. 60, 61). — Dorsal sclerites of segment 8 broadly fused to ventral sclerites; the enclosed membranous area between the dorsal and ventral sclerites found in *mafa* and *galba* reduced to a small pit at the top of a lateral bump. Antevaginally ventral sclerites connected by sclerotization that is continued over short distance into ductus. Postvaginally a wide membranous area, containing a large oblong sclerotization, which starts from the ductus and distally expands strongly before passing into the area spinulosa. Bursa without ornamentation. Papilla analis slightly pointed.

Ecology. — Food plants: Rosaceae.

Distribution. — The combined distribution areas of *sertorius* and *orbifer* comprise the greater part of the Palaearctic Region, from the Atlantic Ocean to Korea and the Amur Region, southwards to NW. Africa, Israel and N. Baluchistan, northwards to the Netherlands, C. Germany, C. Russia and into Siberia. The only other *Spialia* species, which occur within this area, belong to the *phlomidis* group.

Spialia sertorius (Hoffmansegg)

In my 1974 paper on *Spialia* I referred to a paper by Kauffmann (1955), who reported the occurrence of ssp. *sertorius* in Corsica, suggesting that ssp. *sertorius* and ssp. *therapne* are sympatric in this island. Recently I could study the material that prompted Kauffmann to the mentioned paper: 20 specimens in the ZSM, all bearing the following data: Evisa, 15.VI.—2.VII.1954, Leinfest. They are inseparable from ssp. *sertorius*. The long series, all from the same date and locality, suggests the presence of a prospering population. However, the prosperity of the population makes it improbable that it was not found before (and after as well). For this reason I have some doubts about the correctness of the labels.

Spialia orbifer (Hübner)

1. Ssp. *orbifer*. In addition to the 10 ♂ and 6 ♀ from Sicily mentioned in 1974, I have studied 4 ♂ and 1 ♀ from this island (ZSM). They confirm the idea

that there is no pure *orbifer* in Sicily, the female being similar to *sertorius*, the males being closer to *orbifer*. Their sizes fall within the limits mentioned in 1974 for Sicilian specimens.

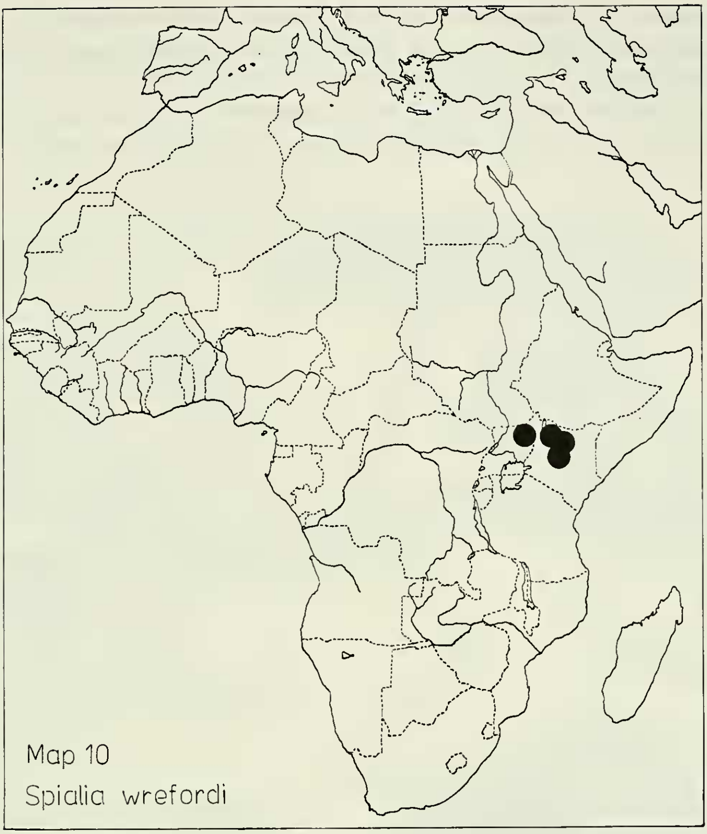
2. Ssp. *carnea*. The 55 additional specimens studied from Afghanistan demonstrate that this subspecies is rather well distributed in this country, but it is scarcely found below 2000 m. It appears that in most specimens the submarginal spot in spaces 4 and 5 on the underside of the hind wing is as large as in other subspecies of *orbifer*, contrary to what was stated in my 1974 paper. In a nice series of 24 ♂ and 2 ♀ from Badakhshan (CN) all males are dark due to almost complete absence of submarginal spots on the upperside, while these spots are well-developed in the two females. On the average the specimens are smaller than *carnea* specimens from other localities, the males measuring 11.8—13.5 mm. The ground colour of the underside of the hind wing is yellow or brown rather than red, and more or less strongly overshaded by black scales. The spots on the underside of the hind wing are well-developed, contrary to the upperside, where in most cases the median band is reduced to an exclamation mark: a white bar closing the cell and a white point in space 2.

f. The *dromus* group

External characters. — Basal cell spot on fore wing upperside present; central cell spot central between basal cell spot and discocellular spot; no spots in spaces 9 and 10; submarginal spots usually all present, but sometimes vague; outer median spot 1b absent, 1c absent or present; inner median spot 1b present, 1c rarely absent. Median spots on hind wing underside all present (except in *paula*, where median spot 6 is absent), forming a continuous band of very diverging shape and direction; submarginal spots 4 and 5 in line with the other submarginal spots. Male without costal fold.

Male genitalia. — Uncus undivided; junction with tegumen slightly marked, no fenestrula. Gnathos dorsally joined to tegumen over short distance, ventrally passing into a semiglobular fold, which is finely spinulose, thus suggesting sclerotization; the fold is medially uplifted, so that there is a left and right part. Anellus dorsally strongly sclerotized to form a roof or a winged structure over the aedeagus. Aedeagus straight or slightly S-shaped, surface smooth. Saccus relatively long. Costal process of valva well-developed, with long spines usually directed cephalad (towards base of valva) or cephalo-dorsad (spines upturned). Cucullus with a fold, that partly conceals the costal process.

Female genitalia. — Segment 8 with two dorsal and two ventral sclerites, separated by membranes. The ventral sclerites may touch each other, but are not conjoined. Membranous postvaginal region with a slight triangular sclerotization that usually imperceptibly passes into the area spinulosa. Ductus usually long and gradually passing into bursa. Bursa without ornamentation. Papilla analis without basal lobe; apophysis posterior usually longer than papilla.



Spialia wrefordi Evans

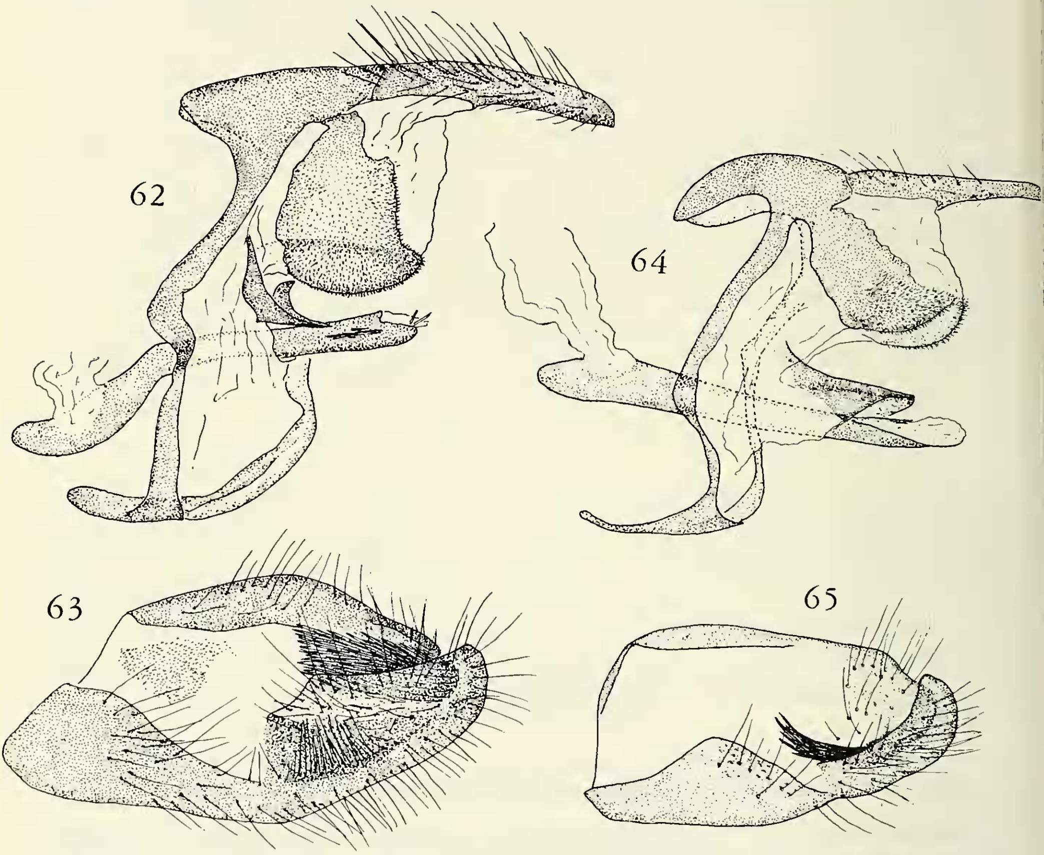
Spialia wrefordi Evans, 1951. — Ann. Mag. Nat. Hist. (12) 4 : 1270—1271 (Kotido, Karamoja, Uganda). Holotype (♂) in the British Museum (Nat. Hist.), London.

External characters (pl. 5 figs. 33, 34). — Easily recognized by the extensive spotting on the upper and undersides of the wings. The very large basal cell spot on the upperside of the fore wing (about twice as long as broad and much larger than the central cell spot) is found in no other *Spialia* species. On the upperside of the hind wing the most distinctive character, apart from the strong development of the spots, is the median spot 1c that runs from vein 1b to vein 2. On the underside of the hind wing the median band is more or less divided by darker veins, especially veins 4 and 7, so that the underside reminds of a strongly spotted *S. colotes*, but the submarginal spots 4 and 5 are not out of line as in that species. ♂ 8.5—11.7 mm, ♀ 10.5—13 mm.

Male genitalia (figs. 62, 63). — Dorsal sclerotization of anellus laterally upturned. Aedeagus S-shaped. Saccus distinctly shorter than uncus. Costal process with straight, horizontal spines, directed cephalad, not upturned. Near base of valva a spinulose area in the membrane between costa and sacculus.

Female genitalia (figs. 70, 71). — Area spinulosa deeply indented, forming a gap that is closed by the distinct, triangular, postvaginal sclerotization. Papilla analis short, broader than long; apophysis posterior short, slightly longer than length of papilla, slightly shorter than width of papilla.

Ecology. — Unknown. The known specimens have been caught during the months April, June and July. Apparently restricted to dry and hot areas.



Figs. 62—65. Male genitalia, lateral aspect, and inside of right valva. 62—63, *S. wrefordi* (Kotido, Uganda). 64—65, *S. paula* (Essexvale, Rhodesia).

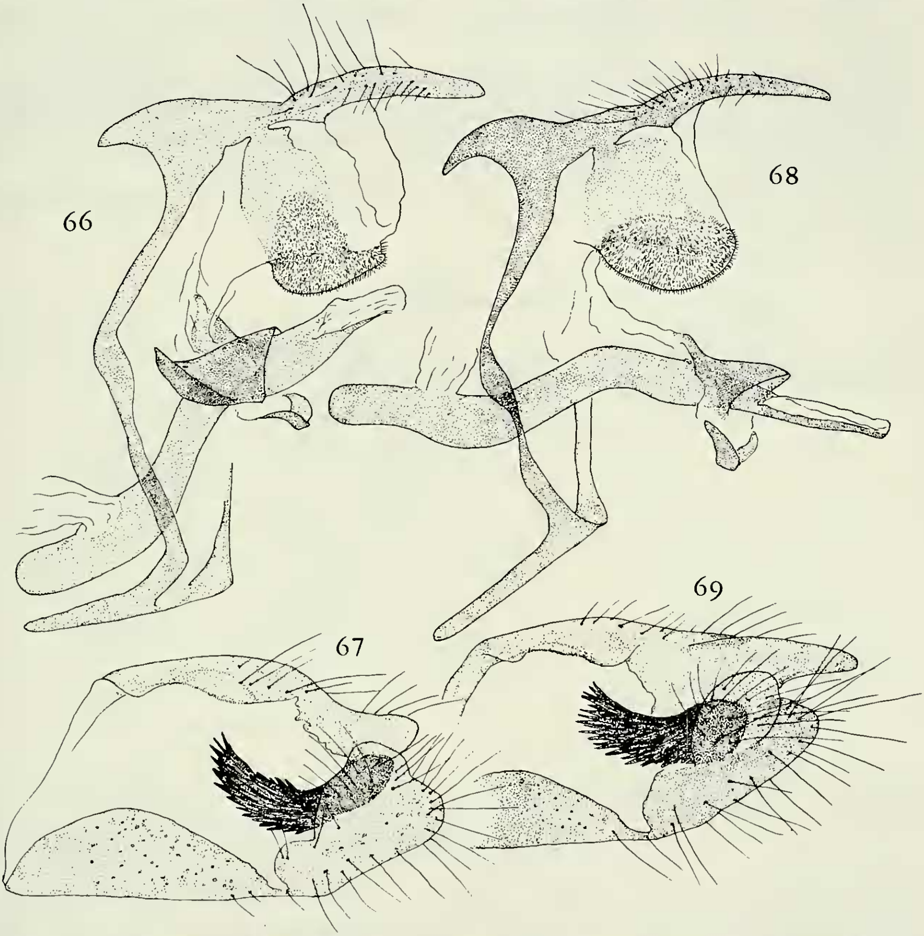
Distribution (Map 10). — Only known from four localities, viz., Kotido (Uganda, Karamoja), Samburu Game Reserve (Kenya, Rift Valley Prov.), Mt. Kulal and Mt. Marsabit (both Kenya, Eastern Prov.). Undoubtedly, this species is more widely distributed in the badly known dry northern parts of Uganda and Kenya.

Material examined. — 19 ♂, 12 ♀ : 18 ♂ (incl. holotype), 10 ♀, Uganda (AMNH, BM, ML, MN); 1 ♂, 2 ♀, Kenya (AMNH, BM, ML).

Spialia paula (Higgins)

Hesperia paula Higgins, 1924. — Trans. ent. Soc. London 1924 : 77, pl. 8 fig. 22 (Bulawayo, Rhodesia). Holotype (♂) in the British Museum (Nat. Hist.), London.

External characters (pl. 5 figs. 35, 36). — This species differs from the other species of the *dromus* group in the absence of median spot 6 on the underside of the hind wing. In this respect it may be confused with *mafa* and *spio,* though these species, and especially *spio,* are usually much larger. However, the shining white of most spots on the underside of the hind wing and the fusion of median spots 1c and 2 on the same wing make the distinction of *paula* not extremely difficult.



Figs. 66—69. Male genitalia, lateral aspect, and inside of right valva. 66—67, *S. ploetzi ploetzi* (Namwamba Valley, Uganda). 68—69, *S. ploetzi occidentalis* (Warri, Nigeria).

In the few specimens studied the length of the fore wing varies in the male from 8.4 to 9.1 mm, in the female from 10 to 10.2 mm.

Male genitalia (figs. 64, 65). — Dorsal sclerotization of anellus laterally bent downwards, forming a roof over the aedeagus. Aedeagus straight. Saccus slightly shorter than uncus. Costa of valva in distal part indistinctly delimited. Costal process narrow, curving upwards, so that the spines point cephalo-dorsad.

Female genitalia (figs. 72, 73). — Ventral sclerites of segment 8 very narrowly conjoined antevaginally. Weak triangular sclerotization in membranous postvaginal area, separated from slightly indented area spinulosa by a narrow membranous band. Papilla analis pointed, longer than wide; apophysis posterior much longer than papilla.

Ecology. — In S. Africa *paula* is on the wing from August to April (Swanepoel, 1953). It usually flies over grassy hill slopes. Food plants have not been recorded.

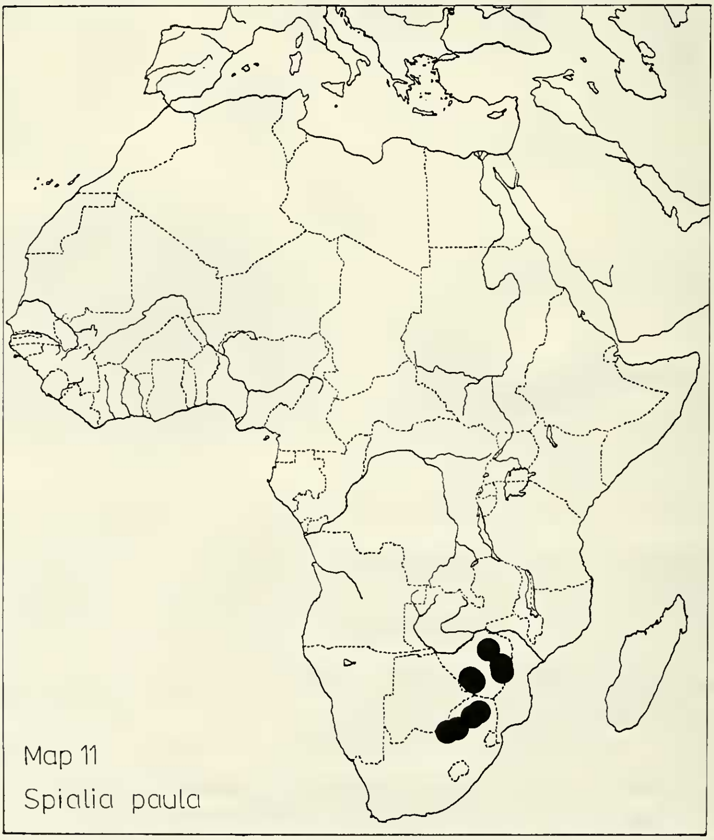
Distribution (Map 11). — A very restricted range, in Transvaal and Rhodesia.

Localities. — Rhodesia: Bulawayo, Essexvale, Filabusi, Gwanda, Penkridge, Salisbury, Umtali (BM, MN, MNHN, NMB). South Africa. Transvaal: Munnik, Pietersburg, Rustenburg, Swartruggens (NMB; Swanepoel, 1953).

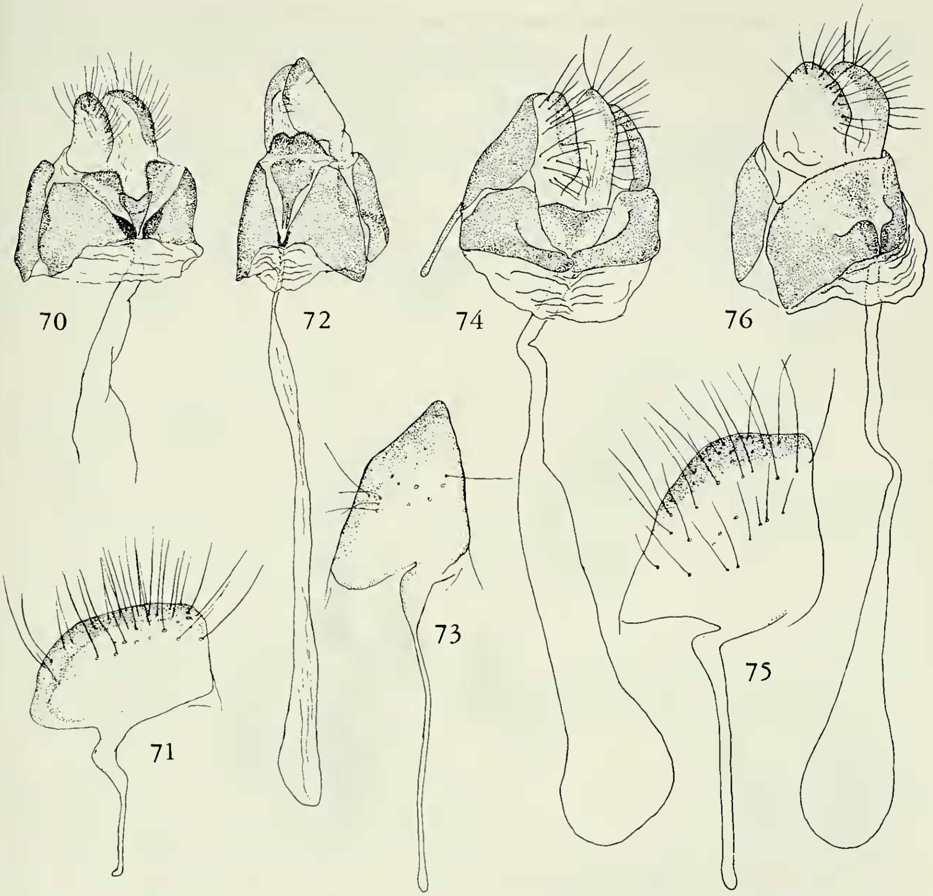
Material examined. — 4 ♂, 2 ♀ : 4 ♂ (incl. holotype), 1 ♀, Rhodesia (BM, MN); 1 ♀, South Africa (BM).

Spialia secessus (Trimen)

Pyrgus secessus Trimen, 1891. — Proc. zool. Soc. London 1891 : 102, pl. 9 fig. 22 (Omrora, Damaraland). Holotype (♂) in the South African Museum, Cape Town.



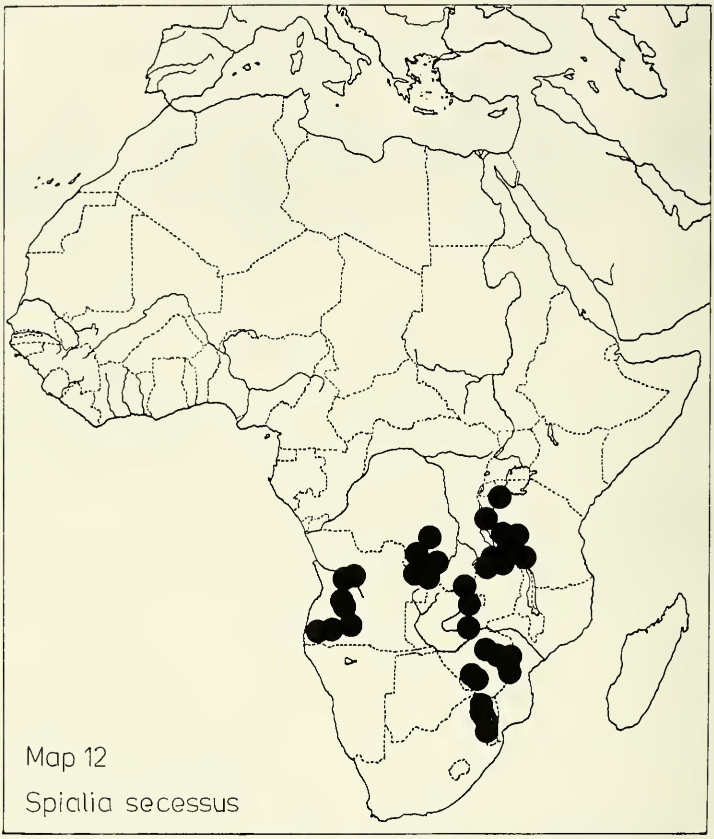
Hesperia secessa forma *trimeni* Aurivillius, 1925. — Hesperidae, in: A. Seitz, The Macrolepidoptera of the World 13 : 564, pl. 75d (Rhodesia). The type of *trimeni* is probably lost; the only *trimeni* in the Naturhistoriska Riksmuseet, Stockholm, is a male from Angola.



Figs. 70—76. Female genitalia, ventral and lateroventral aspect, and papilla analis. 70—71, *S. wrefordi* (Kotido, Uganda). 72—73, *S. paula* (Essexvale, Rhodesia). 74—75, *S. ploetzi ploetzi* (Namwamba Valley, Uganda). 76, *S. ploetzi occidentalis* (Bingerville, Ivory Coast).

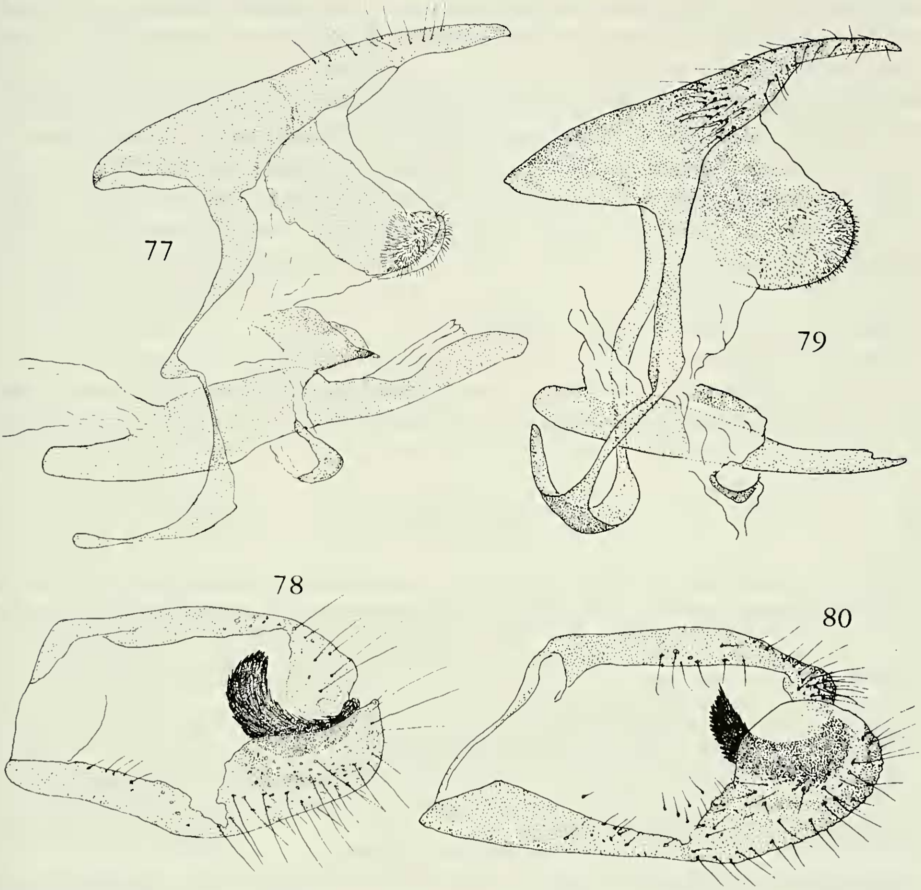
External characters (pl. 5 figs. 37, 38). — This species is unlike any other *Spialia* species on the underside of the hind wing, where the median band is straight and of even width throughout, with the outer margin finely denticulate (i.e. slightly produced along the veins); this denticulation is accentuated by a darkening of the ground colour along the outer margin of the band. The inner margin of the band is less clearly defined. The effect is difficult to express in words, but the photograph gives a good impression, and once having seen a real specimen, it is improbable that one confuses this species with any other *Spialia* species. Moreover, there are two colour forms, one of which is particularly distinct, because the band on the underside of the hind wing is brown instead of white; as the ground colour is also brown, the band is mainly distinguishable by the darkening of the ground colour along its outer margin.

The two colour forms have been named forma *secessus* Trimen (median band on hind wing underside brown) and forma *trimeni* Aurivillius (median band on hind wing underside white or cream-coloured). Aurivillius (1925: 564) supposed these forms to be the result of seasonal variation. This assumption is undoubtedly correct, as their ranges overlap completely and their flight periods are largely separated. However, while Aurivillius considered f. *trimeni* the wet season form, Evans (1937) mentioned f. *secessus* as such. I think Aurivillius was right. Almost all specimens of f. *secessus* examined were collected in July and August, while the bulk of f. *trimeni* examined date from October till February. In the distribution area of the species the rains usually occur in the latter period, while July and August are dry.



There are some exceptions, especially in f. *secessus* of which I have seen single specimens from January, May, June, September and October, while f. *trimeni* may appear as early as September and single specimens are known from April, May and June. Supposing these specimens are correctly labelled, they may be the result of microclimatic differences. The brown band of f. *secessus* occurs in various shades and specimens intermediate between f. *secessus* and f. *trimeni* occur, especially in April-May and September.

Male genitalia (figs. 77, 78). — Gnathos relatively narrow and double semiglobular spinulose fold smaller than in other species of the group. Dorsal sclerotization of anellus upturned laterally. Aedeagus rather thick in central part, laterally slightly expanded in distal part, but apex narrow. Saccus well-developed, but shorter than uncus. Costa of valva distally expanded, mainly in ventral direction. Costal process strongly upturned, spines pointing dorsad. Fold of cucullus not covering base of costal process.



Figs. 77—80. Male genitalia, lateral aspect, and inside of right valva. 77—78, *S. secessus* (Mpanda, Tanzania). 79—80, *S. dromus* (Tabora, Tanzania).

Female genitalia (figs. 81, 82). — Ventral sclerites of segment 8 widely separated near ostium. Sclerotization of postvaginal membranous region slight, but distinct, proximally continued over a short distance in dorsal side of ductus, distally passing into protruding, unindented area spinulosa. Papilla analis obtusely triangular; apophysis posterior nearly 1.5 times as long as papilla.

Ecology. — A species of grassy slopes, flying in probably two, maybe more generations, mainly from July to February, rarely from March to June. Food plants not recorded.

Distribution (Map 12). — From Tanzania and S. Zaïre to Transvaal and Natal.

Localities. — Tanzania: Butler South, Chala (Ufipa), Dunduma, Kampissa, Kasoje, Kassaka River, Katari, Kotuma, Lubalisi, Mahale, Mbisi Forest, Mbosi, Mpanda, Sibweza, Sitebi, Tungamu (Ngara), Wanzizi (BM, ML, MN, MRAC, ZSM). Zambia: L. Bangweolo (Luwingu), High Plateau south of Lake Tanganyika, Kafue Flats, Lofu River, Mporokoso, Ndola (BM, NRS, ZSM; Neave, 1910). Rhodesia: Bulawayo, Essexvale, Gurbi River, Headlands (E. Mashonaland), Hopefountain (nr. Bulawayo), Inyanga Mts., Melsetter, Odzani River (Umtali), Salisbury (BM, NMB). South Africa. Transvaal: Barberton, Graskop, Groenbult, Haenertsburg, Helpmekaar, Munnik, Nelspruit, Shilouvane, White River (BM; Murray, 1959; Swanepoel, 1953). Natal: Natal (BM). Angola: Bailundo, Bihe Distr., Capelongo-Dongo, Cauca, Chitau, Cubal River, Omrora (AMNH, BM, CMP, MNHN, NRS; Trimen, 1891). Zaïre: Bukama, Ditanto, Elisabethville, Kafakumba, Kambove (150—200 mls W of Kambove), Kapanga River, Kapelekese, Karavia, M'Pemba Zeo (Gandajika), Sando (BM, MRAC).

Material examined. — 102 ♂, 42 ♀ : 51 ♂, 18 ♀, Tanzania (BM, ML, MN, MRAC, ZSM); 5 ♂, 3 ♀, Zambia (BM, NRS, ZSM); 5 ♂, Rhodesia (BM, MN); 1 ♂, Natal (BM); 3 ♂, 7 ♀, Transvaal (BM); 7 ♂, 5 ♀, Angola (AMNH, BM, CMP, NRS); 30 ♂, 9 ♀, Zaïre (BM, MRAC).

Spialia dromus (Plötz)

Pyrgus dromus Plötz, 1884. — Mitt. Naturwiss. Ver. Neu-Vorpomm. 45 : 6 (Congo). Type(s) lost. Holland (1896) mistrusted the type-locality given by Plötz, because he supposed *dromus* not to occur "further north than Angola on the West Coast", a very incorrect supposition.

Pyrgus zaira Plötz, 1884. — Mitt. Naturwiss. Ver. Neu-Vorpomm. 45 : 6 (Congo). Type(s) lost.

Syrichthus melaleuca Oberthür, 1912. — Et. Lép. Comp. 6 : 113, fig. 1327 (Kitanga). Holotype (♂) in the British Museum (Nat. Hist.), London.

Syrichthus leucomelas Oberthür, 1912. — Et. Lép. Comp. 6 : 118, fig. 1308 (Mpala, L. Tanganyika). Holotype (♂) in the British Museum (Nat. Hist.), London.

Hesperia dromus var. *elongata* Higgins, 1924. — Trans. ent. Soc. London 1924 : 95 (Makindu, Kenya). Holotype (♂) in the British Museum (Nat. Hist.), London.

Hesperia dromus var. *meridionalis* Higgins, 1924. — Trans. ent. Soc. London 1924 : 95 (Zanzibar). Holotype (♂) in the British Museum (Nat. Hist.), London.

External characters (pl. 5 figs. 39, 40). — This species can be distinguished by the following combination of characters:

a. Fore wing upperside. — Basal cell spot well-defined, rounded; central cell spot midway between basal cell spot and discocellular spot; inner median spots 1b and 1c present, forming a bar from vein 1 to vein 2, outer median spots 1b and 1c absent or 1c visible as a small spot at the outer lower angle of median spot 2.

b. Hind wing underside. — Band of median spots continuous from vein 1b to costa, sharply bent basad in space 2.

The characters of the upperside of the fore wing will usually suffice to distinguish *dromus* from all other *Spialia* species.

There is much variation in the extension of the spots and some forms have received names. In forma *meridionalis* Higgins, the spots are reduced on the upperside and the submarginal spots may be entirely wanting. A specimen without median spots on the upperside of the fore wing except in space 1b, but with well-developed submarginal spots, was described as a new species, *melaleuca*, by Oberthür (1912), but the genitalia of this specimen clearly showed it to belong to *dromus*, of which it appears to be a unique aberration. Another aberrant male in the BM, from Natal, has the spots on the upperside of the hind wing wanting except for the basal cell and small submarginal spots, while most of the spots on the upperside of the fore wing are abnormally large, reminding of forma *taras* of *Pyrgus malvae* L.

A form with the band of median spots on the upperside of the hind wing distinctly continued across space 1c (as on the underside) was named "var. *elongata*" by Higgins (1924). This character is also found in the forma *leucomelas* that was described as a new species by Oberthür (1912) and only differs from *elongata* in the extremely broad band of median spots of the hind wing.

There is also much variation in the length of the fore wing, see under Geographic variation.

Male genitalia (figs. 79, 80). — Dorsal sclerotization of anellus flat or medially slightly depressed. Aedeagus straight, cylindrical. Saccus shorter than uncus. Costal process of valva long, upturned, with long spines pointing ventrad and cephalo-dorsad; fold of cucullus covers greater part of costal process, including its base.

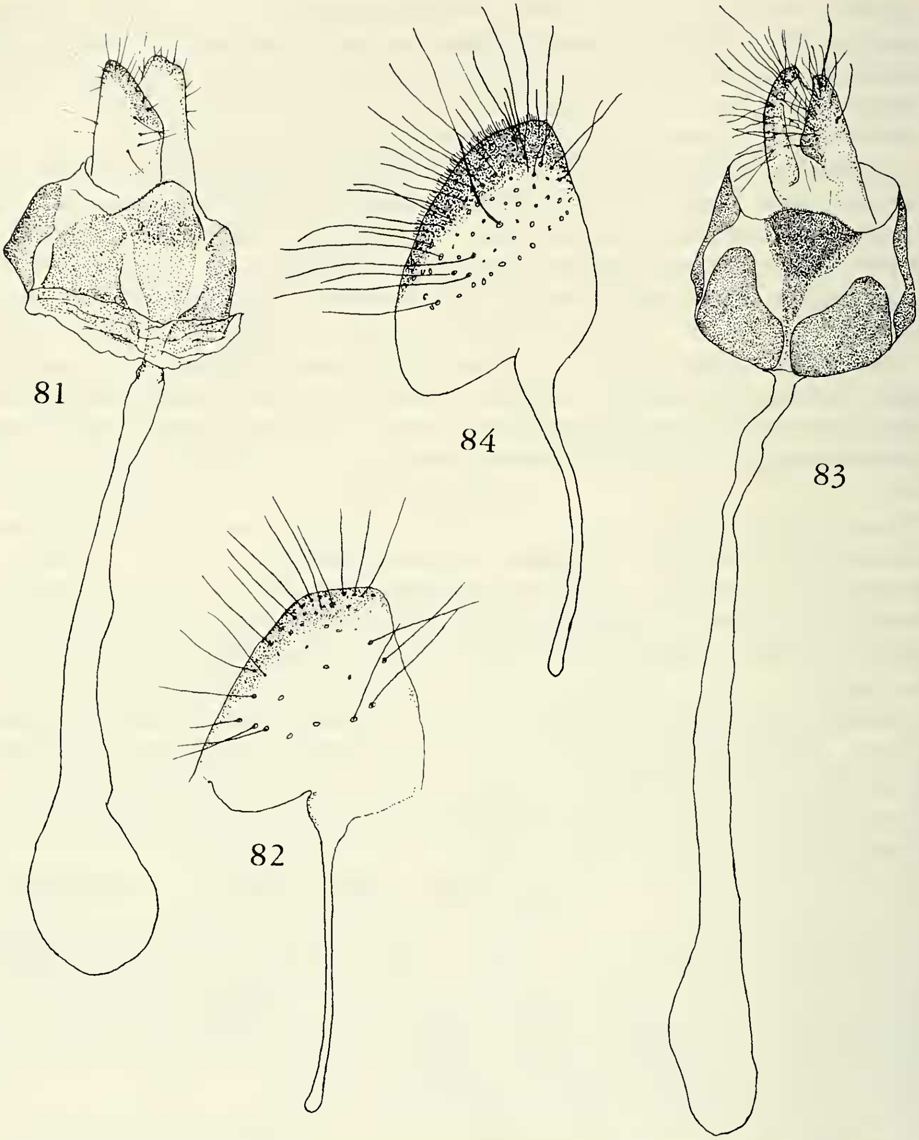
Female genitalia (figs. 83, 84). — Ventral sclerites of segment 8 well-defined, separated from each other and from the dorsal sclerites by a membranous gap. Postvaginal membranous region with triangular sclerotization that is especially distinct in its narrow part near the ostium and that passes into the unindented area spinulosa. Papilla analis rather triangular; apophysis posterior somewhat longer than papilla.

Ecology. — *S. dromus* is more at home in wooded areas than in open savanna and can particularly be encountered at forest fringes, along forest paths, etc., though not in dense forest. It has been found flying in all months of the year. Recorded food plants are *Triumfetta tomentosa* Boj. and *rhomboidea* Jacq. (Tiliaceae) (Murray, 1959; Gifford, 1965).

Distribution (Map 13). — One of the most widely distributed *Spialia* species in Africa, occurring from Natal to Ethiopia and Senegal. Although it is apparently less common than *diomus* in S. Africa, *dromus* appears to be the commoner species in the rest of Africa. It reaches its greatest abundance in Central and East Africa and it is outnumbered by *spio* in West Africa. The absence of records from many regions (e.g. Liberia, Lindsey & Miller, 1965; Guinea and Ivory Coast, Berger, 1962) is undoubtedly due to incomplete collecting.

Geographic variation. — There appears to be a slight clinal variation in the length of the fore wing (♂ 9.1—13.8 mm) and the extension of the white spots. In general, the larger and better marked specimens are found in the south, but there is very much overlap in the length of the fore wing and the extension of the spots in the various regions. Although specimens with large spots are most common in the southern part of Africa (north to Tanzania), the form *elongata* is most common in the western and northern parts of the distribution area. The large range of overlap makes it impossible to delimit subspecies.

Localities. — Ethiopia: Cherosh Wonz, Fich (Shoa Prov.), Gimera to N. end of L. Rudolf (BM; Carpenter, 1935). Sudan: Jebel Marra (W. Darfur), Talanya (Vambio) (BM). Kenya: throughout (AMNH, BM, CMP, ML, MN, MNHN).

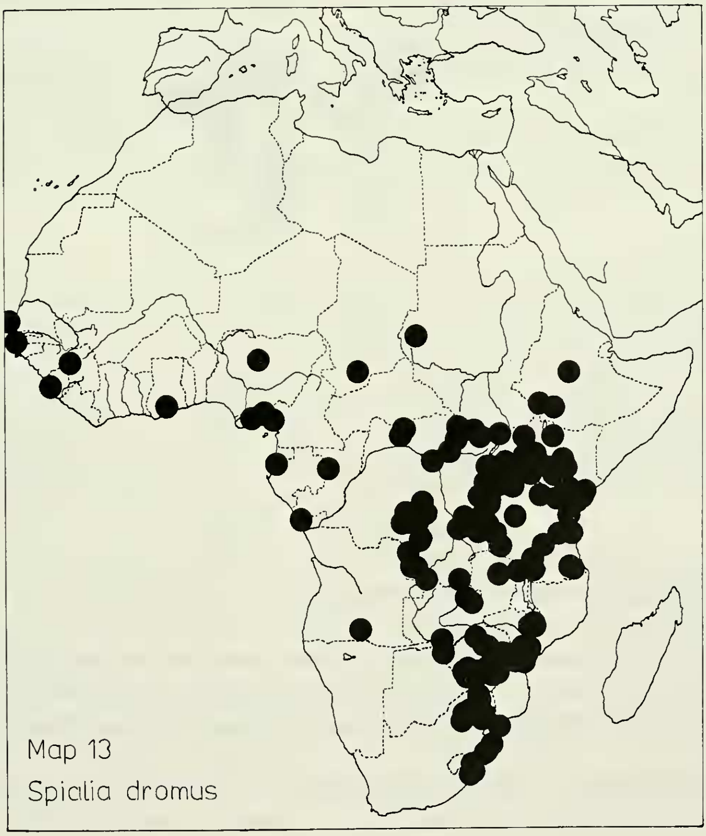


Figs. 81—84. Female genitalia, ventral aspect, and papilla analis. 81—82, *S. secessus* (Mpanda, Tanzania). 83—84, *S. dromus* (Natal).

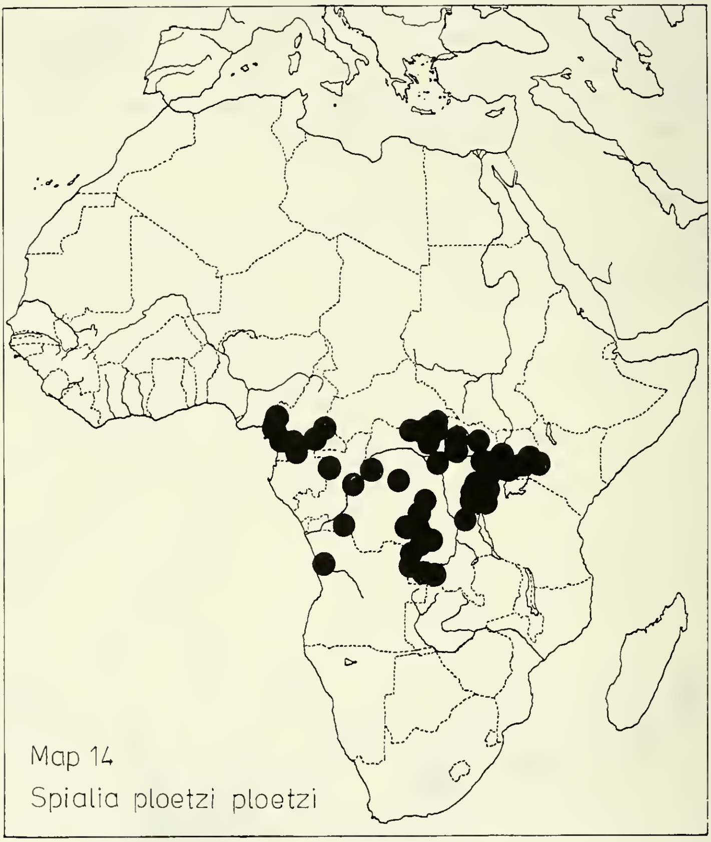
Uganda: throughout (AMNH, BM, CMP, MN). Tanzania: throughout (AMNH, BM, ML, MN, MNHN, MRAC, NMB, ZSM). Rwanda: Kitengi, Ruhengeri (ML, MRAC). Burundi: Bukcba-Usumbura, Kitega, Muyaga (MRAC; Rebel, 1914). Zambia: throughout (BM, NMB, USNM, ZSM; Neave, 1910). Rhodesia: throughout (BM, ML, MRAC, NMB, USNM). Malawi: throughout (BM, CMP, NMB, USNM; Gifford, 1965). Mozambique: Amatonga Forest, Andrada, Delagoa Bay, Dondo Forest, Gorongoza, Inhaminga, Lourenço Marques, Salone Forest, Serra

Rotanda (BM, ML, MNHN, NMB, ZSM). South Africa. Transvaal: Barberton, Chuniespoort, Graskop, Konatipoort, Louis Trichardt, Lydenburg Distr., Malta Forest, Mariepskop, Mica, Munnik, Nelspruit, Olifantsrivier, Pietersburg, Potgietersrust, Pretoria, Saltpan, Sibasa, Tubex, Warmbaths, Woodbush, Zoutpansberg (NMB; Swanepoel, 1953). Natal: Amahlongwa, Durban, Eshowe, Greytown, Hluhluwe, Howick, Isipingo, Ismont, Karkloof, Maritzburg, Umbloti, Umkomaas (AMNH, BM, CMP, ML, MNHN, MRAC, NMB, ZSM; Swanepoel, 1953). Angola: Ehanda (BM; Trimen, 1891). Zaïre: throughout (AMNH, BM, CMP, MNHN, MRAC; Holland, 1920). Congo-Brazzaville: Etoumbi (Berger, 1967). Gabon: Gabon River (Trimen, 1889). Tchad: Fort Archambault (MNHN). Cameroun: Bamenda (BM). Nigeria: Aba, Kaduna, Obuda Ranch (E. Nigeria) (BM, MN, ZSM). Ghana: Likpe (BM, MRAC). Sierra Leone: Sierra Leone (BM). Guinea: "Guinée française" (MNHN). Senegal: Dakar, Oussony, Sandiaba, Tabi près Bignona (BM, CMP, MNHN; Berger, 1968).

Material examined. — 618 ♂, 242 ♀ : 1 ♂, 1 ♀, Ethiopia (BM); 2 ♂, Sudan (BM); 102 ♂, 37 ♀, Kenya (AMNH, BM, CMP, ML, MN); 39 ♂, 13 ♀, Uganda (AMNH, BM, CMP, MN); 155 ♂, 52 ♀, Tanzania (AMNH, BM, ML, MN, MRAC, ZSM); 2 ♂, 1 ♀, Rwanda (ML, MRAC); 26 ♂, 14 ♀,


Map 13
Spialia dromus

Burundi (MRAC); 2 ♂, Zambia (USNM, ZSM); 12 ♂, 4 ♀, Rhodesia (BM, MN, USNM); 37 ♂, 16 ♀, Malawi (BM, CMP, USNM); 24 ♂, 9 ♀, Mozambique (BM, ML, ZSM); 55 ♂, 44 ♀, South Africa (AMNH, BM, CMP, ML, MRAC, ZSM); 18 ♂, 7 ♀, Angola (BM); 112 ♂, 31 ♀, Zaïre (AMNH, BM, CMP, MRAC); 1 ♂, Congo-Brazzaville (MRAC); 14 ♂, 5 ♀, Nigeria (BM, MN, ZSM); 3 ♂, 5 ♀, Ghana (BM, MRAC); 9 ♂, 3 ♀, Sierra Leone (BM); 4 ♂, Senegal (BM, CMP).



Map 14
Spialia ploetzi ploetzi

Spialia ploetzi (Aurivillius)

Hesperia Ploetzi Aurivillius, 1891. — Ent. Tidskr. 12 : 227 (Cameroun). For synonymy, see subspecies.

The nomenclatural and taxonomic confusions about this species have been dealt with in a previous paper (De Jong, 1977). The species shows a marked geographic variation. The subspecies recognized have generally been considered separate species and Higgins (1924) created a species group for them ("*Hesperia plötzi* group").

External characters. — On the underside of the hind wing the median spots in spaces 3 to 7 and the submarginal spots in spaces 1c and 2 conjoin to form an oblique white bar from about the middle of vein 8 to the termen in space 1c or 2. By this character *S. ploetzi* is easily distinguished from all other *Spialia* species. On the upperside of the hind wing the marked median band which is sharply broken along vein 3 by the direction of the median spot 4—5 and the basad shift of median spot 2, is distinctive. Length of fore wing 11.4 — 13 mm.

Male genitalia. — Spinulose area of gnathos extending dorsad to slightly beyond the middle of the gnathos. Dorsal sclerotization of anellus folded over aedeagus like a roof, but laterally bent upwards. Aedeagus long, S-shaped, surface smooth. Saccus about as long as uncus. Costa of valva extended distad. Costal process large, curving upwards, spines pointing cephalo-dorsad. Fold of cucullus covering about basal third of costal process.

Female genitalia. — Ventral sclerites of segment 8 touching near ostium, but not conjoined. Postvaginal membranous area wide, with slight triangular sclerotization that imperceptibly passes into area spinulosa. Latter with straight or slightly wavy distal edge. Papilla analis with obtuse apex; apophysis posterior less than 1.5 times as long as papilla.

Ecology. — *S. ploetzi* is the only *Spialia* species confined to the forest. Specimens are known from all months of the year. Food plants unknown.

Distribution. — Confined to the forest belt from Sierra Leone to Western Kenya. The southern limit appears to run through N. Angola, S. Zaïre and along the north side of Lake Tanganyika. East of this lake, *ploetzi* does not appear to occur south of Burundi. The northern limit presumably runs through the Central African Republic.

Geographic variation. — There is a marked variation in the extension of the spots, the male and female genitalia. Two subspecies can be recognized.

Spialia ploetzi ploetzi (Aurivillius)

Hesperia Ploetzi Aurivillius, 1891. — Ent. Tidskr. 12 : 227. Type locality: Cameroun, environs of Douala, see De Jong (1977). Lectotype (♂) in the Naturhistoriska Riksmuseet, Stockholm.

Hesperia zebra Rebel, 1914. — Ann. k.k. naturh. Hofmus. Wien 28 : 271—272, pl. 22 figs. 52, 53 (NW of Lake Tanganyika). Holotype (♂) in the Naturhistorisches Museum, Vienna. Junior primary homonym of *Hesperia zebra* Butler, 1888 (which is now also placed in *Spialia*).

Hesperia rebeli Higgins, 1924. — Trans. ent. Soc. London 1924 : 101. Replacement name for *Hesperia zebra* Rebel, 1914. Evans (1937) stated that the type of *rebeli* is in the British Museum (Nat. Hist.), and he labelled, indeed, a specimen from Uganda as type (nr. H. 892). This was, however, an incorrect action, for the type of *rebeli* Higgins should be the same as that of *zebra* Rebel, as Higgins only proposed a replacement name.

External characters (pl. 6 figs. 41, 42). — On the whole, this eastern subspecies is more extensively spotted than the western one. In detail, the differences are as follows:

1. on the upperside the spots are larger, especially the central cell spot on the fore wing and the submarginal spots on both wings;
2. on the fore wing the series of submarginal spots is less sinuous;
3. on the upperside of the hind wing the submarginal spots 5 and 6 are strongly developed, forming two white streaks (in the western form they are scarcely visible);

4. on the underside of the hind wing the submarginal spots 5 and 6 are fused into a white streak from median spot 7 to the end of vein 5 (this streak is at most faintly indicated in the western form);

5. in addition to this streak the veins are usually overlaid with light scales, so that the underside of the hind wing has a striped appearance;

6. median spot 2 on the underside of the hind wing is usually indistinct and sometimes absent (in the western form usually very distinct and often more conspicuous than the lower part of the median band).

According to Higgins (1924) the ground colour of the upperside is paler in the eastern form. I cannot confirm this observation, but it may be true for fresh material.

Eastern specimens of ssp. *ploetzi* generally have larger spots on the upperside, especially on the hind wing, and often a lighter ground colour on the underside of the hind wing, due to a denser light superscaling. There is, however, much overlap in these characters and it does not appear to be sensible to recognize further subspecies.

Male genitalia (figs. 66, 67). — Costa of valva not extending beyond tip of cucullus.

Female genitalia (figs. 74, 75). — Narrow, medio-proximal parts of ventral sclerites (i.e. the parts nearest the ostium) at least two times as long as broad.

Distribution (Map 14). — The eastern part of the range of the species, from W. Cameroun eastward. The westernmost localities known are Kumbo and Bamenda in W. Cameroun, close to the Nigerian frontier and formerly Nigerian territory. The easternmost localities are situated in the forest remains in the west of Kenya. In the Nairobi Museum there is a specimen labelled "W. Atomo, Mombasa"; I could not find W. Atomo on any map or in any gazetteer, the only name approaching it is Watamu, about 100 km north of Mombasa. It would be highly interesting if *ploetzi* really occurred there.

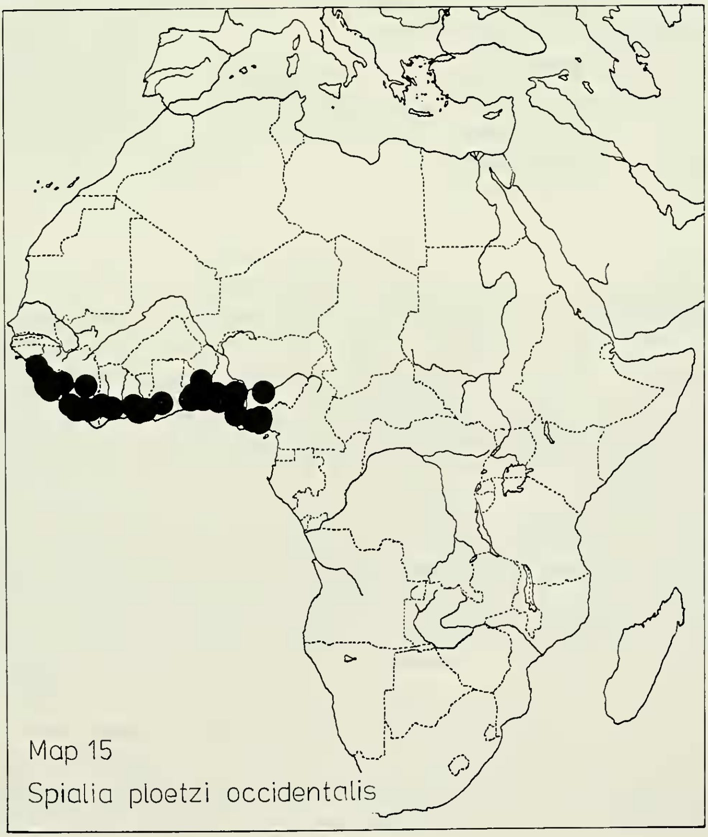
Localities. — Kenya: Kaimosi, Kakamega Forest, Malaba (Kabras), ? Mombasa (W. Atamo) (MN, USNM). Uganda: Bwamba Forest, Budongo Forest, Bufunbo Forest, Entebbe, Hoima, Impenetrable Forest, Jinja, Kalinzu Forest, Kamengo, Kanaba Gap, Katera, Kayonza Forest (Kigezi), Kazi, Mafuga Forest (Kigezi), Mbarara, Mt. Kokanjero, Muhende, Mulange, Namwamba Valley, Rutenga Forest (Kigezi), Toro (AMNH, BM, CMP, MN, MRAC, NMB). Rwanda: Cyangugu, Kisaba Forest (BM, ML). Burundi: Bugarama, Bulumbura, Bururi, Kitega, Ruvuvu River (BM, MRAC). Zaïre: Bambesa, Bena-Tshiadi, Bokala à Busanga, Buta, Dungu, Eala, Epulu Forrst, Gamangui, Goma-Rutshura, Itimbiri-Dingila, Itoko à Sombe, Kabongo, W. of Kambove, Kaniama, Kapanga, R. Kapelekese, Katako-Kahudi, Katako-Kombe, Lake Kivu, NW. of Lake Tanganyika, Lodja, Lowa-Nduba, Lufupa River, Lukolela, Luluabourg, Lusambo-Batempa, Mbudi, Medje, Moto, Nioka, Nyamunyunya (Mulungu), Omotumba, Paulis, Ruwenzori, Sandoa, Stanleyville, Tshibinda, Tshikunia, Tshiole, Uele, Utshudi, Yakoma (AMNH, BM, CMP, MN, MRAC, NMB, USNM; Heron, 1909; Higgins, 1924; Holland, 1920; Neave, 1910; Rebel, 1914). Angola: N'Dalla Tando (BM). Congo-Brazzaville: Etoumbi (MRAC; Berger, 1967). Gabon: Lastousville, Oyem (MNHN, MRAC).

Rio Muni: Nkolentangan (ZMHB). Central African Rep.: Boukolo M'Baiki (Oubangui-Chari) (MRAC). Cameroun: Akom, Bamenda, Batouri Distr., Bitye (Ja River), Buea, Bule Country, Chang, Ebogo s. le Nyong, Efulen, Ekutu, Elat, Kribi, Lolodorf, Lomié, Metet, Penderu, Sakbayeme (Sanaga River), Zoatoupsi (20 km W. of Yaoundé) (AMNH, BM, CL, CMP, MNHN MRAC, NMB, NRS, USNM, ZWM; Condamin, 1960).

Material examined. — 262 ♂, 69 ♀ : 4 ♂, 3 ♀, Kenya (MN, USNM); 85 ♂, 27 ♀, Uganda (AMNH, BM, CMP, MN, MRAC); 2 ♂, Rwanda (BM, ML); 6 ♂, 1 ♀, Burundi (BM, MRAC); 67 ♂, 21 ♀, Zaïre (AMNH, BM, CMP, MN, MRAC, USNM); 5 ♂, Angola (BM); 1 ♂, Congo-Brazzaville (MRAC); 2 ♂, Gabon (MNHN, MRAC); 1 ♂, Rio Muni (ZMHB); 1 ♂, Centr. Afr. Rep. (MRAC); 88 ♂, 37 ♀, Cameroun (AMNH, BM, CMP, MNHN, MRAC, NRS, USNM, ZSM).

Spialia ploetzi occidentalis De Jong

Spialia ploetzi occidentalis De Jong, 1977. — Ent. Ber., Amst. 37 : 43 (Ghana). Holotype (♂) in the Rijksmuseum van Natuurlijke Historie, Leiden; paratypes in the British Museum (Nat. Hist.), London, and the Naturhistoriska Riksmuseet, Stockholm. This subspecies is generally known in the literature as the species *Spialia ploetzi*.



External characters (pl. 6 figs. 43, 44). — Less extensively spotted than ssp. *ploetzi;* for details, see under that subspecies.

Male genitalia (figs. 68, 69). — Costa of valva projecting well beyond tip of cucullus.

Female genitalia (fig. 76). — Medio-proximal part of ventral sclerites about as long as broad.

Distribution (Map 15). — The western part of the range of the species, from Sierra Leone to E. Nigeria. Specimens of this subspecies recorded from localities further east are probably incorrectly labelled, see De Jong (1977).

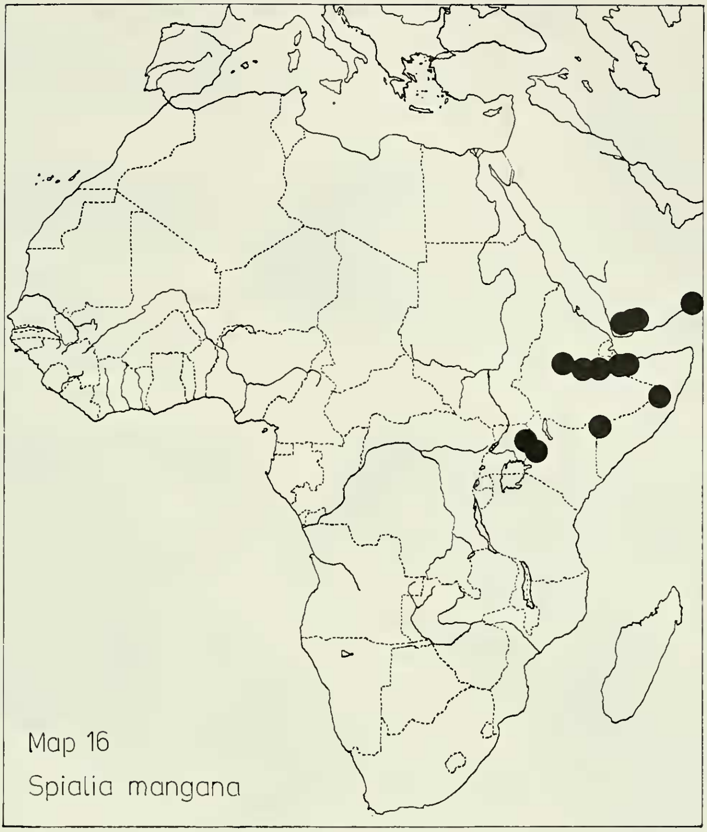
Localities. — Cameroun (?): "Cameroons" (MNHN). Nigeria: Afikpo, Anambara Creek, Cape Coast Castle, Ebele, Ibadan, Iporia-Ilara Div., Kabba Prov., Lagos, Lokkoh, Oban, Ogruga, Old Calabar, Oshodi, Warri (BM, CMP, MN, MNHN; Higgins, 1924). Dahomey: Porto Novo, Dahomey Interior (MNHN). Togo: Missahohé (= Misa-höhe) (ZSM). Ghana: Asuchari, Kumasi, Likpe, Odumase Swamp, Sunyani (BM, ML, MRAC). Ivory Coast: Abengourou, Abidjan, Adiopodoumé, Bingerville, Issia, Séleu (BM, MN, MNHN, MRAC; Berger, 1962). Liberia: Bigtown, Ganta, Harbel, Kpain, Maloubli, Monrovia, Penoke, Zorzor (BM, CMP; Lindsey & Miller, 1965; Picard, 1950). Sierra Leone: Freetown, Ka Yima, Moyamba, "Sierra-Leone" (BM, MNHN, NRS, ZSM; Holland, 1896). Guinea: Forecariah, Tondon (C. Dubreka) (BM, MNHN; Berger, 1962).

Material examined. — 108 ♂, 38 ♀ : 1 ♂, ? Cameroun (MNHN); 13 ♂, 9 ♀, Nigeria (BM, CMP, MN); 1 ♂ Togo (ZSM); 21 ♂ (incl. holotype of *occidentalis*) 5 ♀, Ghana (BM, ML, MRAC); 29 ♂, 9 ♀, Ivory Coast (BM, MN, MRAC); 10 ♂, 3 ♀, Liberia (BM, CMP); 31 ♂, 12 ♀, Sierra Leone (BM, NRS, ZSM); 2 ♂, Guinea (BM).

g. The *delagoae* group

External characters. — Fore wing without basal cell spot on upperside, at most some white scales forming a small dash along the cubital vein; central cell spot not remarkably close to end of cell; no spots in spaces 9 and 10; submarginal spots present or absent. Median band on underside of hind wing straight or winding, continuous from space 1c to space 8, more or less parallel to termen; submarginal spots 4—5 (if present) in line with the other submarginal spots. Male without costal fold.

Male genitalia. — Uncus undivided or bipartite apically; junction with tegumen indicated by a narrow, less strongly sclerotized band, medially broadening to a fenestrula. Gnathos dorsally joined to tegumen over a shorter or longer distance or free from tegumen, the dorsal edge often folding outwardly; broadly sclerotized, ventrally usually with stronger sclerotization and some short spines; left and right part of gnathos ventrally joined by a membrane that is usually smooth, but may be slightly spinulose and folding upward medially. Anellus with very strong dorsal sclerotization and spines. Juxta relatively large. Aedeagus straight or slightly curved, with ventral, cylindrical, spined excrescence in distal half; coecum short or absent. Saccus relatively short, i.e. shorter than uncus.

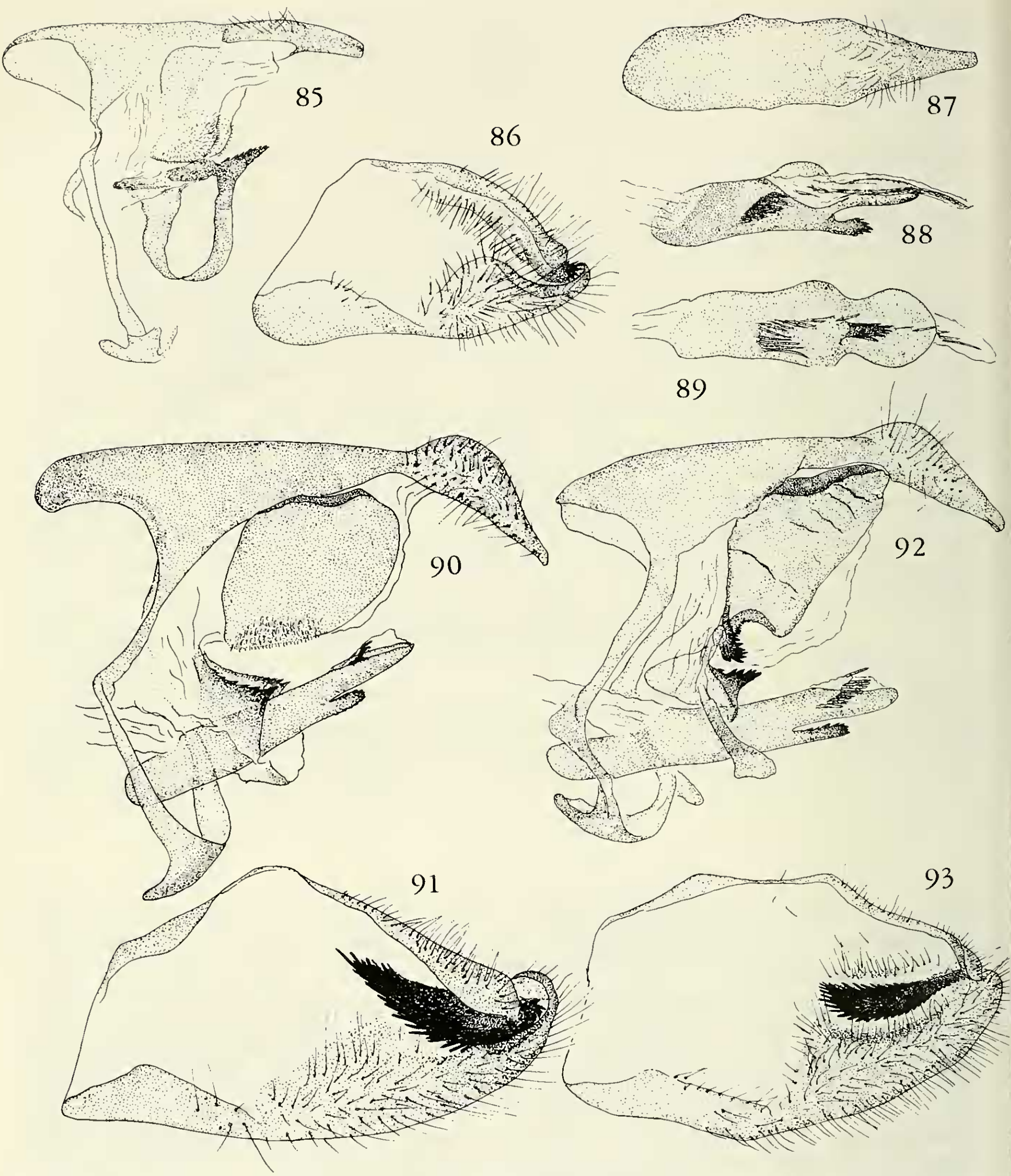


Costa of valva narrow; costal process various, usually well-developed. Cucullus excavated to receive costal process or forming a small fold, that does not cover the costal process.

Female genitalia. — Segment 8 with two small dorsal sclerites, which are invisible in ventral sight; ventral surface occupied by a single large sclerite covering the whole surface or with small membranous areas distally from the ostium to the left and to the right. In all but one species there is no noticeable sclerotization antevaginally. Just behind the ostium the sclerite may protrude in two small keels. Small spines of area spinulosa in some species visible at the distal edge of the ventral sclerite. Ductus long, gradually broadening into bursa; ductus and bursa without sclerotizations or spines. Papilla analis without basal lobe, short, broader than long; apophysis posterior short, about as long as or shorter than width of papilla.

Spialia mangana (Rebel)

Hesperia mangana Rebel, 1899. — Sber. Akad. Wiss. Wien 1899 : 360 (Ras Fartak, S. Yemen). Holotype (♀) in Naturhistorisches Museum Wien (Vienna, Austria).



Figs. 85—89. Male genitalia of *S. mangana* (Bihendula, Somalia). 85, lateral aspect. 86, inside of right valva. 87, dorsal aspect of uncus and tegumen. 88, lateral aspect of aedeagus. 89, ventral aspect of aedeagus. Figs. 90—93. Male genitalia, lateral aspect, and inside of right valva. 90—91, *S. nanus* (Sheldon, S. Africa). 92—93, *S. delagoae* (Muden, S. Africa).

External characters (pl. 6 figs. 45, 46). — An unmistakable species by the complete absence of basal and submarginal spots on the upper and underside of both wings. On the upperside the ground colour is evenly dark brown, on the underside of the hind wing the ground colour of the basal part is usually of a lighter shade than between the median band and the termen. A good figure was given by Rebel (1907).

There is much variation in size, ♂ 7.5 — 9.9 mm, ♀ 8.1 — 11 mm, but the material is too limited to show whether this variation is individual, seasonal or geographic.

Male genitalia (figs. 85—89). — At junction of uncus and tegumen a long, triangular fenestrula. Gnathos connected with tegumen by a membrane; ventrally a double, semiglobular, spinulose fold (cf. *dromus* group). Sclerotization in dorsal part of anellus forming a spined prong to the left and the right, ventrally conjoined to the juxta. Aedeagus short and broad, with a strong, spined excrescence medio-ventrally beyond the middle. Just beyond the ventral excrescence the aedeagus is constricted laterally and beyond this constriction it widens to a flat, almost circular apex; coecum absent. Costal process small, with a few short spines radiating distad. Cucullus excavated to form a narrow fold that scarcely covers a part of the costal process.

Female genitalia (figs. 94, 95). — Ventral sclerites of segment 8 conjoined antevaginally by a thick, bumpy sclerotization. Slight sclerotization in postvaginal area, the membranous area separating the ventral sclerites. Area spinulosa slightly indented at distal edge. Papilla analis dorso-distally rather pointed.

Ecology. — Nothing is known of the ecology of this possibly rare skipper. The studied specimens date from all months, except February and March.

Distribution (Map 16). — Confined to the southern part of the Arab peninsula, Ethiopia, Somalia, N. Kenya and N. Uganda.

Localities. — Yemen: Ta'izz (BM; Gabriel, 1954). South Yemen: Ahdaherma, Dhala, Jebel Jihaf, wadi east of Jebel Ma'fari, Moola Mutar, Ras Fartak (BM; Gabriel, 1954; Rebel, 1899, 1907). Ethiopia: Dire Daoua, Fich Shoa Prov., Meiso (BM, MNHN; Carpenter, 1935). Somalia: Bihendula, Galkayu, Gan Linah, Hargeisa, Mandera, Mudugh (BM, MN). Kenya: Kacheleba, Kenailmat (Suk) (BM, MN). Uganda: Cholol (Karamoja) (MN).

Material examined. — 19 ♂, 8 ♀ : 1 ♂, Yemen (BM); 3 ♂, 3 ♀, South Yemen (BM); 4 ♂, 2 ♀, Ethiopia (BM); 6 ♂, 2 ♀, Somalia (BM, MN); 3 ♂, 1 ♀, Kenya (MN); 2 ♂, Uganda (MN).

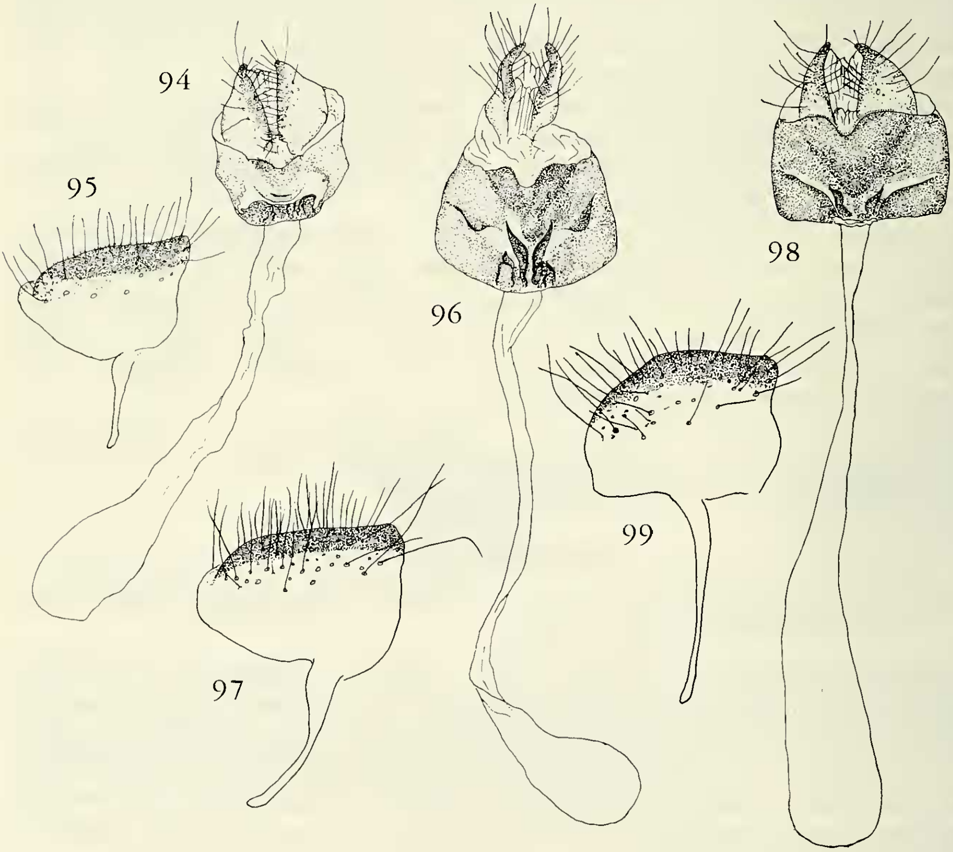
Spialia nanus (Trimen)

Pyrgus nanus Trimen, 1889. — South African Butterflies 3 : 290 (Malmesbury, Cape). Holotype (♂) in the British Museum (Nat. Hist.), London.

External characters (pl. 6 figs. 47, 48). — By the combination of the absence of a basal cell spot on the upperside of the fore wing and a continuous band of median spots on the underside of the hind wing, this species is easily recognized as a member of the *delagoae* group. The basal cell spot on the underside of the hind wing is absent or very faintly indicated, the median band is very winding and runs from the end of space 8 through a double curve to about the middle of the distal part of space 1c.

There is much variation in size (♂ 8.5 — 11 mm) and spotting. The submarginal spots on the upperside may be almost absent; the spots 2 and 4—5 and regularly also 1c and 3 of the median spots are present on the upperside of the hind wing. The ground colour of the underside of the hind wing varies from warm yellow to brown. Although there are two generations per year, Swanepoel (1953) does not mention seasonal variation.

Male genitalia (figs. 90, 91). — A triangular fenestrula at junction of uncus and tegumen. Uncus with a longitudinal keel. Gnathos not fused to tegumen, consisting of two sclerotized plates, which curve outside in the upper part, so that in dorsal view the gnathos protrudes laterally. In the ventral part of the gnathos the sclerotization is fainter and here is a finely spinulose area. Anellus with strong, dorsally spined sclerotization, partly surrounding the aedeagus and membranously connected with the juxta. Aedeagus straight, with short coecum and a relatively long, ventral, spined projection; large cornuti present. Costa of valva narrow; costal process much larger than costa, directed to base of valva, slightly bent upwards, strongly spined. Cucullus excavated, forming a very narrow fold that does not cover the costal process.



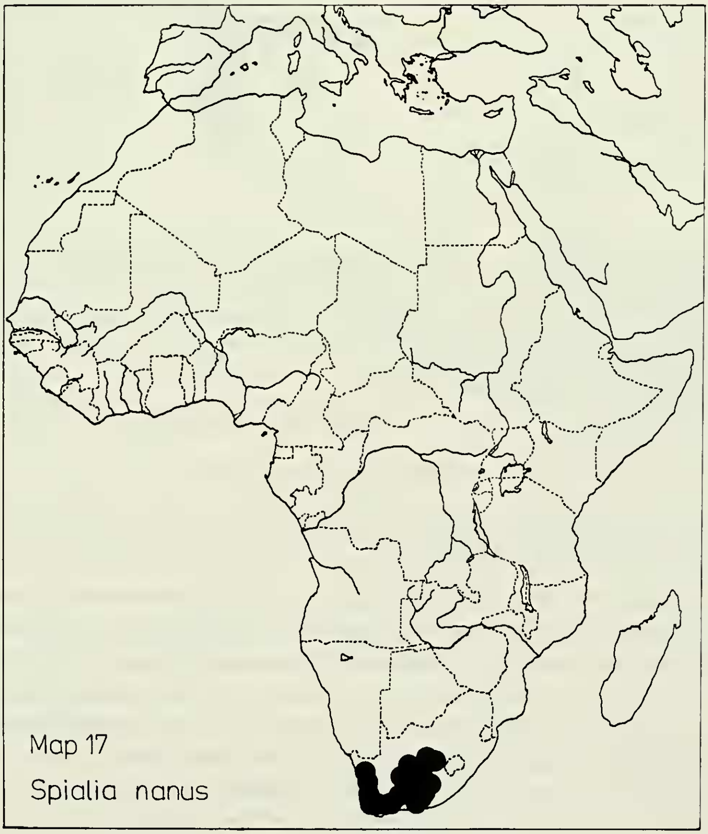
Figs. 94—99. Female genitalia, ventral aspect, and papilla analis. 94—95, *S. mangana* (Dhala, S. Yemen). 96—97, *S. nanus* (Paarde Berg, S. Africa). 98—99, *S. delagoae* (S. Africa).

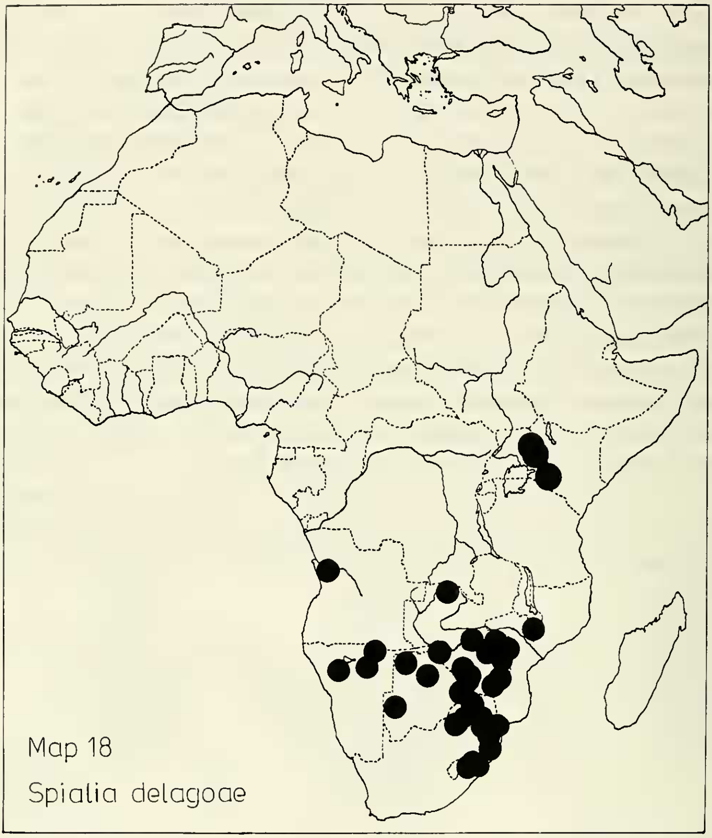
Female genitalia (figs. 96, 97). — Ventral sclerites of segment 8 not conjoined antevaginally, folded alongside the ostium to a few ridges. Postvaginally there is a short and narrow membranous area to the left and to the right of the ostium, enclosed by the ventral sclerites, which are fused and form small folds overlapping the end of the membranous areas. The ventral sclerites include the triangular postvaginal sclerotization. Area spinulosa deeply indented at distal edge. Papilla analis with upper edge rather straight.

Ecology. — This species is at home in the Karroo bushveld of the Cape Province, South Africa, where it can be found almost anywhere, on the flats and along mountain slopes. There are two generations per year, the main flight periods being September—October and March—April (Swanepoel, 1953). As food plants the following species have been recorded (Murray, 1959): *Hermannia* species (Sterculiaceae), *Pavonia macrophylla* and *Hibiscus aethiopicus* (Malvaceae).

Distribution (Map 17). — Confined to South Africa, where it has been found in the Cape Province and the western Orange Free State.

Localities. — South Africa. Cape Province: De Aar, Addo, Beaufort West, Bitterfontein, Calitzdorp, Cape Town, Carlton, Carnarvon, Clanwilliam, Colesberg, Cookhouse, Cradock, Deelfontein, Dunbrody, Graaf-Reinet, Kamieskroon,





Katzenberg Hill, Kimberley, Klaver, Malmesbury, Mamre, Matjesfontein, O'okiep, Paarde Berg, Paarl, Prieska, Rosemead, Sheldon, Slang Hoek Mts., Somerset East, Springbok, Steynsburg, Uitenhage, Vanrhijnsdorp, Worcester (BM, CMP, ML, MN, MNHN, NMB; Swanepoel, 1953). Orange Free State: Bloemfontein (AMNH, BM, NMB; Swanepoel, 1953).

Material examined. — 27 ♂, 10 ♀, South Africa (AMNH, BM, CMP, ML).

Spialia delagoae (Trimen)

Pyrgus delagoae Trimen, 1898. — Trans. ent. Soc. London 1898 : 15 (Delagoa Bay). Holotype (♂) in the South African Museum, Cape Town.

External characters (pl. 7 figs. 49, 50). — This species closely resembles *nanus* by the absence of the basal cell spot on the underside of the hind wing, but the straight median band is a reliable differentiating character. Of the other species of the group, only *mangana* has no basal cell spot on the underside of the hind wing, but that species is easily distinguished by the absence of submarginal spots on upper and underside. The ground colour of the underside of the hind wing is usually dark olive-green. There is some variation in size (♂ 9.9 — 11.6 mm) and extension of spots. On the upperside of the hind wing the median spots 2 and

4—5 are always present, often also 3, sometimes 1c indicated by white scales, 6 always absent.

Male genitalia (figs. 92, 93). — Triangular fenestrula at junction of uncus and tegumen. Uncus with a longitudinal keel, in dorsal view apex slightly expanded. Gnathos dorsally strongly curved outward and projecting laterally; ventral sclerotization stronger than in *nanus*, forming a strongly spined ventral projection. Fultura superior smooth. Dorsal sclerotization of anellus consisting of a strongly spined, pointed structure to the left and to the right, the two parts connected by a strongly incurving, slightly sclerotized fold that is connected dorsally to the gnathos and the fultura superior. Aedeagus straight; coecum longer than thick; ventral projection large, 4—5 times as long as thick; apex flat, but not expanded; a series of subequal cornuti present. Costa of valva very narrow, distally slightly expanded. Costal process very large, almost straight, at apex slightly upturned, pointing towards base of valva, strongly spined. Cucullus hollowed to receive the costal process, not forming a fold.

Female genitalia (figs. 98, 99). — Very much like *nanus*, but sclerotized ridges near ostium smaller and no flaps of ventral sclerites overlying the end of the membranous strips; area spinulosa possibly somewhat wider. Apophysis posterior relatively long, longer than width of papilla.

Ecology. — In South Africa it is a species of the bushveld, that may be found sipping from wet mud or fresh baboon dung (Swanepoel, 1953). There are no records on its habitat in more northern areas. *S. delagoae* is on the wing throughout the year, but in South Africa it is most abundant in February-March and August-September. Food plants have not been recorded.

Distribution (Map 18). — From N. Kenya and N. Uganda to Transvaal and Natal. At the moment the northern populations appear much isolated.

Localities. — Kenya: Kacheleba, Kedong (MN). Uganda: Amudat (MN). Zambia: Solwezi (Higgins, 1924). Rhodesia: Bazely Bridge (SW. Umtali), Bulawayo, Chirinda Forest (Chipinga), Dotts Drift (Lower Sabi Valley), Essexvale, Guzi Forest, Gwanda, Inyanga Mts, Matetsi, Mtoko, Nyamadzi R., Nyamandhlovu, Odzi R., Salisbury, Sanyati Valley, Umtali, Vumba Mts, West Nicholson (BM, MN, NMB, USNM). Malawi: Mlanje (Gifford, 1965; Higgins, 1924). Mozambique: Delagoa Bay (BM, MNHN; Trimen, 1898). Botswana: Hothlotane, Macloutsi, 55 mls E. of Maun, Ngamiland, 55 mls W. of Tsane (BM, MNHN, NMB). Swaziland: Gollel (NMB). South Africa. Transvaal: Bandolierkop, Barberton, Chuniespoort, Dendron, Haenertsburg, Munnik, Ohrigstad, Palabora, Pietersburg, Rita, Shilouvane, Vivo, Warmbaths, Zoutpansberg (BM, CMP; Swanepoel, 1953). Natal: Estcourt, Hluhluwe, Kearsney, Letsibele, Mhlosinga, Middeldrift, Muden, Tugela R., Weenen (BM, CMP; Swanepoel, 1953). Cape Province: Lobabi (MN). Namibia: Groot-fontein, Okawango, Otjitambi, Ovikokonva (SMW). Angola: Dondo (Quanza River) (BM).

Material examined. — 49 ♂, 19 ♀ : 3 ♂, 1 ♀, Kenya (MN); 1 ♂, Uganda (MN); 14 ♂, 4 ♀, Rhodesia (BM, MN, USNM); 2 ♂, Mozambique (BM, MNHN); 1 ♂, Botswana (MNHN); 24 ♂, 10 ♀, South Africa (BM, CMP, MN); 3 ♂, 4 ♀, Namibia (BM, SMW); 1 ♂, Angola (BM).

Spialia zebra (Butler)

Pyrgus zebra Butler, 1888. — Ann. Mag. Nat. Hist. (6) 1 : 207—208 (Koteer, Chittar Pahar). For synonymy, see subspecies.

External characters (pl. 7 figs. 51, 52). — The presence of a basal cell spot and submarginal spots on the underside of the hind wing distinguishes this species from all other species of the group except *depauperata*. According to Higgins (1924) *zebra* (under the name *bifida*) and *depauperata* are almost indistinguishable, but in fact the identification is not very difficult if we pay attention to the following differences:

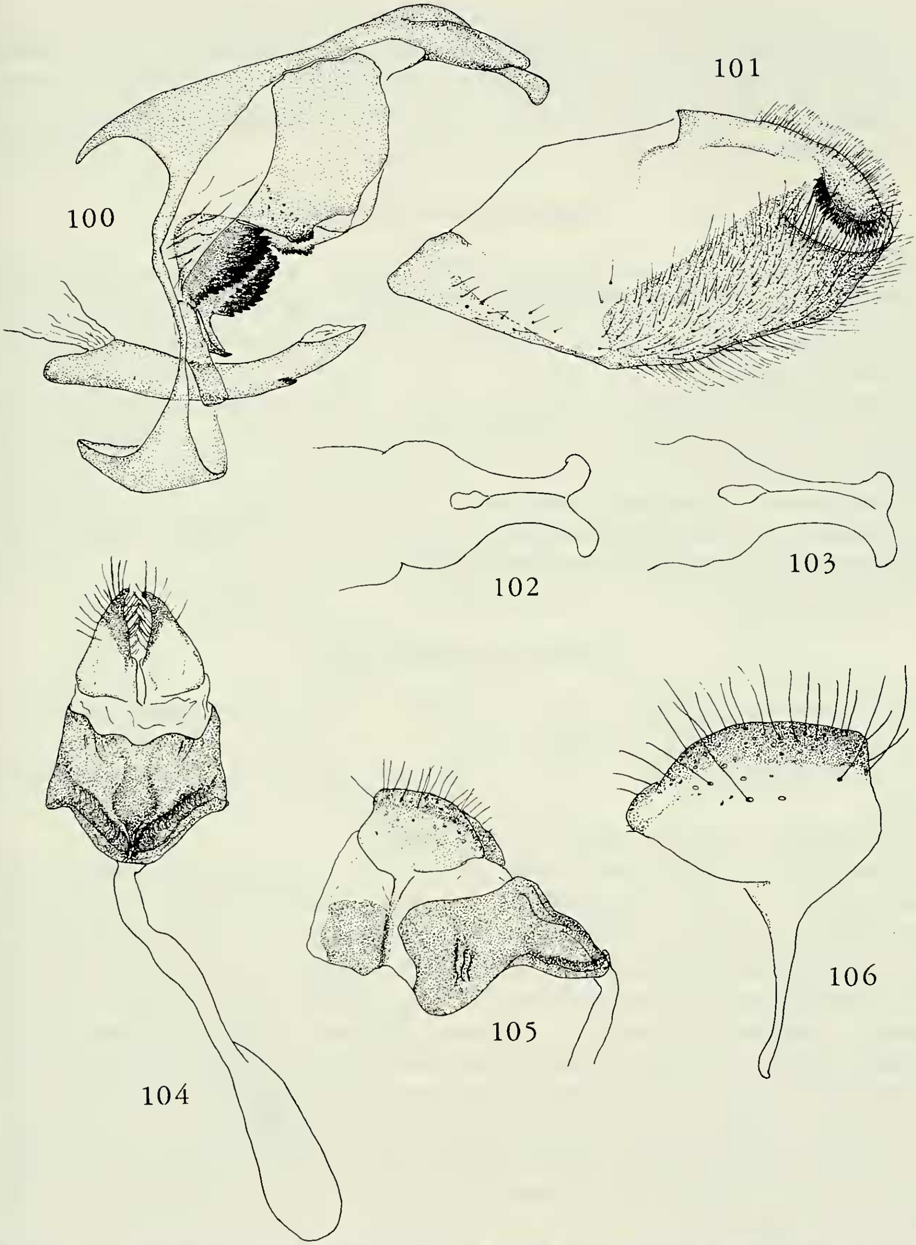
1. on the average, *zebra* is smaller, ♂ 9.7—11.5 mm, as against *depauperata* ♂ 10.4—13.8 mm;
2. in *zebra* the median spots 2 and 4—5 on the upperside of the hind wing are usually the only median spots present, although 3 may be more or less indicated; in *depauperata* the median spots on the upperside of the hind wing form a more or less straight band from vein 2 to vein 7, crossed by the dark veins 3, 4 and 6. I never met with serious difficulties in distinguishing between *zebra* and *depauperata,* but if one is not sure about the identification of a male, a clearing of the tip of the abdomen will soon reveal the difference in the uncus.

There is some variation in the extension of the spots. The submarginal spots on the upperside are sometimes very reduced, but always visible, at least in part. The ground colour of the underside of the hind wing is of a greyish green tinge.

Male genitalia (figs. 100—103). — Uncus bifid at apex, more or less hammer-like in dorsal (and ventral) view, left and right parts with slightly inflated apices. At proximal end of distinct, longitudinal keel of uncus, a small and more or less oblong fenestrula. Gnathos separated by very narrow membranous strip: ventrally slightly more strongly sclerotized and with some small spines, passing into an inwards sclerotized fold that forms a shallow sac and is flanked laterally by a large number of very coarse spines; more ventrally this sclerotization forms two small pointed processes, lying over the dorsal surface of the aedeagus, as in *depauperata,* but much smaller. Aedeagus gently curved upwards; coecum slightly longer than wide; ventral process small, inconspicuous, except for the short spines. Distal end of costa of valva covering part of costal process. Latter not very conspicuous, with radiating spines, in proximal part with some very coarse spines, but not such a distinct, separate proximal part as in *depauperata*.

Female genitalia (figs. 104—106). — Ventral sclerites of segment 8 fused into a single sclerite, postvaginally with a low elevation that is pear-shaped in ventral view. In the proximal part, to the right and to the left of the ostium, the sclerite is excavated; laterally it has a few narrow, protruding ridges. No membranous post-vaginal area. Area spinulosa slightly indented at distal edge. Ductus plus bursa relatively short. Apophysis posterior not longer than width of papilla, relatively straight.

Ecology. — In Kenya I found this species rather numerous along dry paths in more or less open landscape, with scarce vegetation on coral rocks near Ukunda, south of Mombasa. The specimens were flying especially during the hottest time of the day and were not easy to collect, as they often flew very low, sometimes not



Figs. 100—103. Male genitalia of *S. zebra*. 100—102, lateral aspect, inside of right valva, and dorsolateral aspect of uncus, of ssp. *bifida* (Ukunda, Kenya). 103, dorsolateral aspect of uncus of ssp. *zebra* (Pakistan). Figs. 104—106. Female genitalia, ventral and lateral aspect, and papilla analis, of *S. zebra bifida* (Ukambani, Kenya).

more than a few centimeters above the ground. In Kenya, specimens have been found during all months of the year. In India, *zebra* appears to fly mainly in April, May and June, but the material is scarce.

Sevastopulo (1974) records *Melhamia* (Sterculiaceae) as food plant.

Distribution (Map 19). — Highly discontinuously distributed, in East Africa/ South Yemen and Northwest Himalayas.

Geographic variation. — The African and Asian populations differ slightly in the male genitalia. Externally both forms are similar.

Spialia zebra zebra (Butler)

Pyrgus zebra Butler, 1888. — Ann. Mag. Nat. Hist. (6) 1 : 207—208 (Koteer, Chittar Pahar). Holotype (♂) in the British Museum (Nat. Hist.), London.

Hesperia hellas De Nicéville, 1889. — Journ. Bombay Nat. Hist. Soc. 4 : 177, pl. B (Campbellpore). Holotype (♂) may be in the collection of the Zoological Survey of India, Calcutta, but I could not get exact information.

Male genitalia (fig. 103). — Uncus apically slightly indented, the two parts of the apex projecting laterally, so that in dorsal view the uncus is more or less T-shaped.

Distribution. — Northwest Himalayas.

Localities. — Pakistan: Campbellpore; Koteer, Chittar Pahar; Punjab (Butler, 1888; De Nicéville, 1889; Swinhoe, 1913; BM).

Material examined. — 6 ♂ (incl. holotype), 1 ♀, Pakistan (BM).

Spialia zebra bifida (Higgins)

Hesperia bifida Higgins, 1924. — Trans. ent. Soc. London 1924 : 111—113 (Nairobi). Holotype (♂) in the British Museum (Nat. Hist.), London.

Male genitalia (fig. 102). — Uncus deeply indented apically, Y-shaped in dorsal view.

Distribution. — East Africa and South Yemen.

Localities. — South Yemen: Wadi Tiban (NW of Jebel Jihaf) (Gabriel, 1954; BM). Somalia: 20 miles S of Berbera, Bihendula (BM). Ethiopia: Bukuru Bridge (BM). Sudan: Tembura (BM). Kenya: Athi Bridge, Besil (= Bissil), Chepalungu, Diani, Elmenteita, Escarpment, Fourteen Falls, Gilgil, Hoey's Bridge, Kacheleba, Kakamega, Kangondi, Kibwezi, Kima, Kitale, Kitosh, Kitui, Landjoro, Lokichogio, Lucania, Machakos, Makindu, Makueni, Malaba, Mombasa, Mount Elgon, Mulango, Nairobi, Nairobi-Garissa Road, Nandi Plateau, Nanyuki, Ngong, Nyali, Ologorsailie, Shimoni, Sotik, Soy, Suna, Taveta, Trans Nzoia, Twiga, Ukunda, Upper Kuja Valley, Voi, Wangi, Watamu, Yala River (AMNH, BM, CMP, ML, MN, MNB, MNHN, NRS, USNM); Shimba Hills (Sevastopulo, 1974). Uganda: Kotido (MN). Tanzania: Dar-es-Salaam, Geita, Mount Meru, Oldeani, River Himo (BM, ML, MN, MNHN).

Neave (1910) recorded *zebra* from Zambia (Fort Jameson, Luangwa Valley), but this observation concerns *depauperata*, according to three specimens of Neave in the collection of the Hope Department of Entomology, Oxford.

Material examined. — 126 ♂, 56 ♀ : 1 ♀, South Yemen (BM); 2 ♂, Somalia (BM); 1 ♂, 1 ♀, Ethiopia (BM); 1 ♂, Sudan (BM); 116 ♂ (incl. holotype), 53 ♀, Kenya (AMNH, BM, CMP, ML, MN, MNHN, NRS, USNM); 1 ♂, Uganda (MN); 5 ♂, 1 ♀, Tanzania (BM, ML, MN, MNHN).

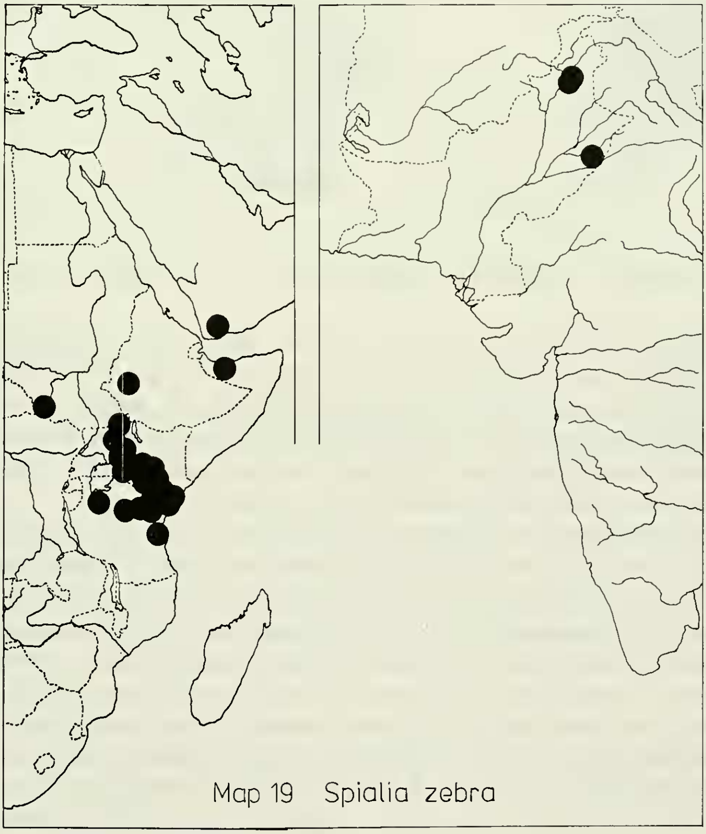
Note. During a recent examination of five males from Mount Elgon (Kenya) two males proved to have the uncus only slightly indented, thus being similar to ssp. *zebra*. More material from the northern part of East Africa as well as from Pakistan is needed to establish the constancy of the difference between the subspecies recognized.

Spialia sataspes (Trimen)

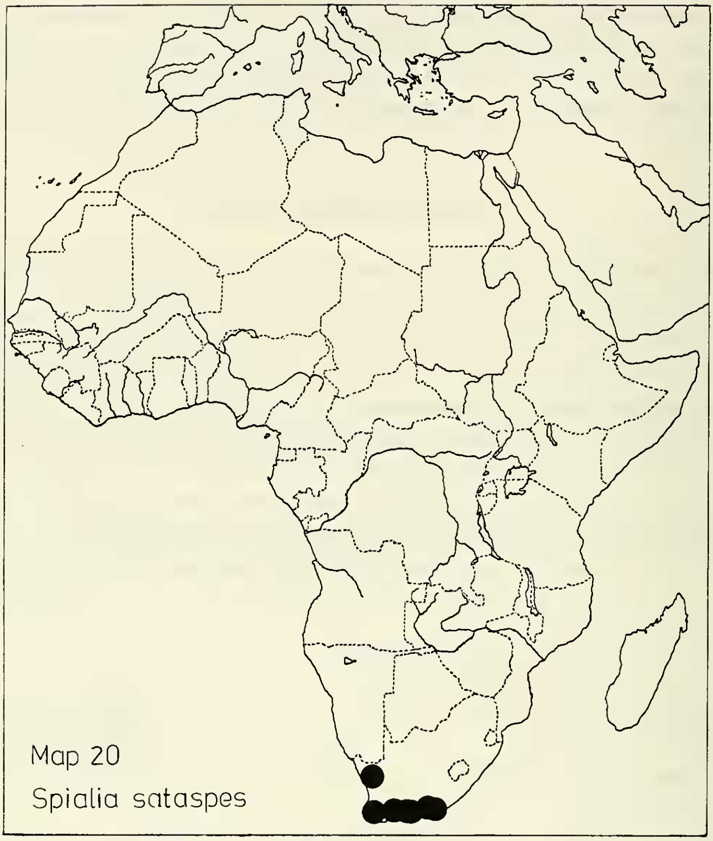
Pyrgus sataspes Trimen, 1864. — Trans. ent. Soc. London 1864 : 178—179 (Plettenberg, Cape Prov.). Holotype (♂) in the British Museum (Nat. Hist.), London.

Trimen (1866) described the same species under the same name again as new.

External characters (pl. 7 figs. 53, 54). — The main differentiating character of this species is the absence of submarginal spots on the underside of the hind wing. This is also the case in *mangana,* but that species lacks the basal cell spot on the underside of the hind wing. The lastmentioned character also distinguishes *sataspes* from *nanus* and *delagoae*. Difficulties may arise with specimens of *zebra* and *depauperata,* in which the submarginal spots on the underside of the hind wing are faint, but in such cases the less straight median band on the underside of the hind



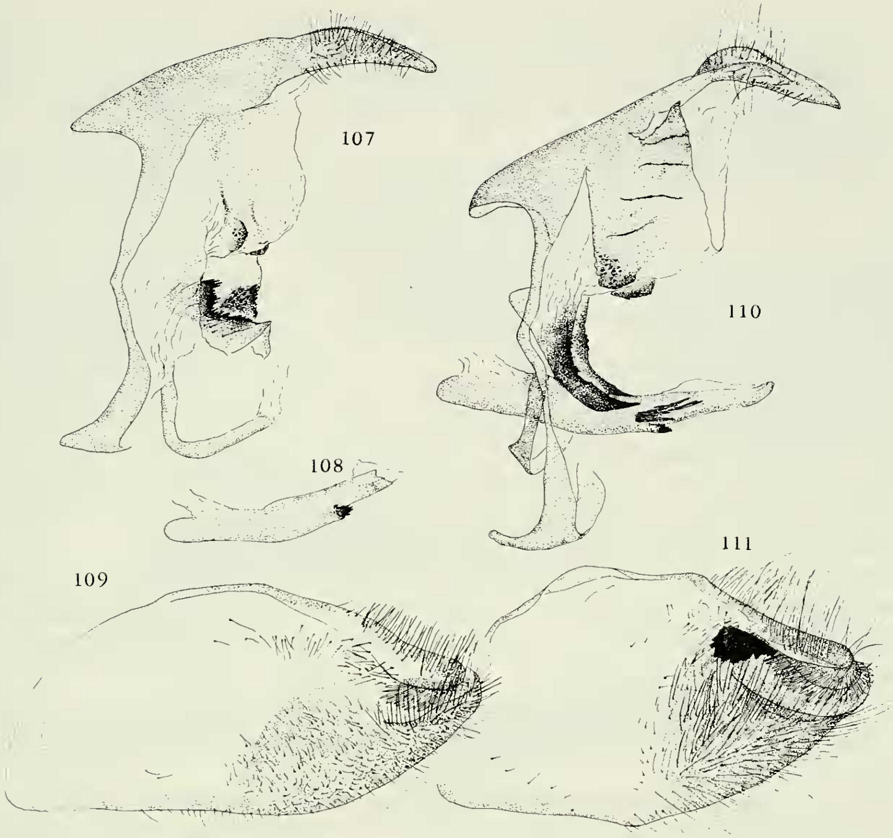
Map 19 Spialia zebra



wing in *sataspes* is helpful. In doubtful cases an examination of the genitalia is necessary.

There is little variation in size (♂ 9.1—11.5 mm) and in extension of the spots. Sometimes the submarginal spots on the upperside are absent. On the upperside of the hind wing the median spots 2 and 4—5 are always present and 1c and 3 are often indicated, while 6 is very rarely visible as a few white scales (contrary to *depauperata,* which usually has a distinct median spot 6). The ground colour of the underside of the hind wing is tawny.

Male genitalia (figs. 107—109). — Fenestrula at junction of uncus and tegumen relatively small. Uncus with longitudinal keel and slightly inflated apex. Gnathos fused to tegumen, not very much curving outward, ventrally somewhat extended to form a rounded sclerotized flap with a few small knobs. Fultura superior smooth, below gnathos passing into the extensive dorsal sclerotization of the anellus. This sclerotization curves inward proximad to form a shallow sac, laterally strongly spined, and then it folds roof-like over the aedeagus. Aedeagus slightly bent in the middle; coecum scarcely longer than wide; ventral process short, about as long as wide, with strong spines. Costa of valva expanding distally; costal process small, mainly consisting of a series of spines radiating from the ventro-distal end of the



Figs. 107—111. Male genitalia, lateral aspect, aedeagus, and inside of right valva. 107—109, *S. sataspes* (Cape Town, S. Africa). 110—111, *S. depauperata australis* (Muden, Natal).

costa. Cucullus broadly developed, dorsally excavated to receive the costal process.

Female genitalia (figs. 112—114). — Ventral sclerites of segment 8 fused into a single sclerite, covering the ventral and lateral parts of the segment. No antevaginal sclerotization. Just behind ostium two flap-like longitudinal outgrowths. Laterally a few very small folds. Area spinulosa broad, distal edge slightly impressed. Papilla analis much broader than long, apophysis posterior shorter than width of papilla.

Ecology. — Mainly found in grassy spots on mountain slopes, where it skips about and feeds on flowers. It is on the wing from the middle of October to February, and seems to be most abundant in November (Swanepoel, 1953). Food plants are *Hermannia* species (Sterculiaceae), *Pavonia macrophylla* and *Hibiscus aethiopicus* (Malvaceae) (Murray, 1959).

Distribution (Map 20). — Confined to South Africa, ranging from the Cape peninsula eastwards to the Grahamstown district and with a few localities outside this range. It was recorded by Butler (1901) from Mombasa, but this observation probably relates to *zebra*.

Localities. — South Africa. Cape Province: Addo, Assegaibosch, Bathurst, Brak R., Cape Town, Coega, Grahamstown, Knysna, Ladysmith, Lion's Head, Llandudno, Muizenberg, Outeniqua Mts, Plettenberg, Port Alfred, Port Elizabeth, Sea Point (Cape Town), Signal Hill, Simonstown, Springbok, St. James, Zwartkops (BM, MN, NMB; Swanepoel, 1953).

Material examined. — 21 ♂ (incl. holotype), 11 ♀ , South Africa (BM, MN).

Spialia depauperata (Strand)

Hesperia ferax var. *depauperata* Strand, 1911. — Mitt. zool. Mus. Berlin 5 : 304 (Msamwia, between Lake Rukwa and Lake Tanganyika, S. Tanzania; not Msamusia, as stated by Evans, 1937).

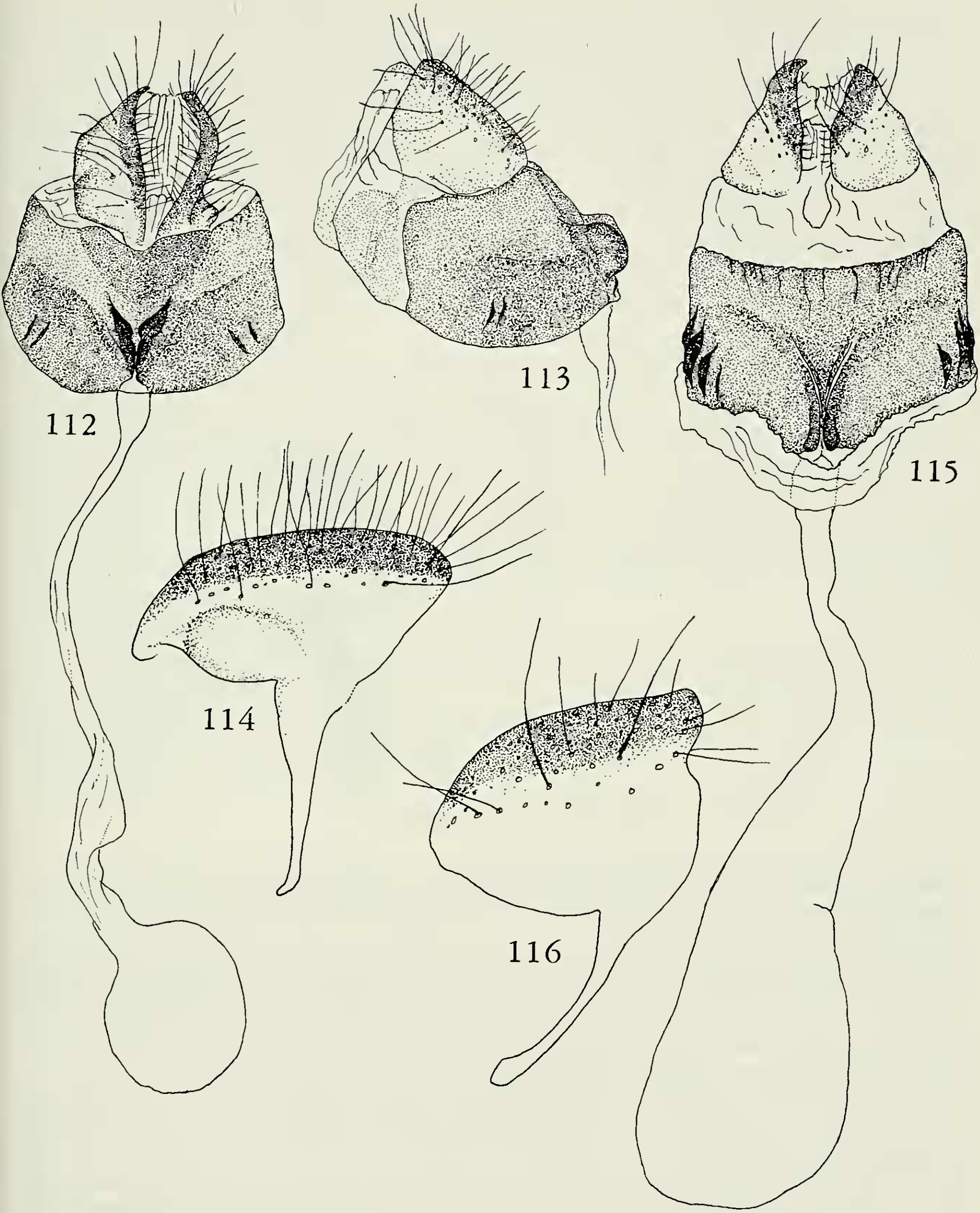
External characters (pl. 7 figs. 55, 56). — The largest species of the group; I saw only one specimen (♂) which was smaller than 10.8 mm, while the largest male measured 13.8 mm. Its size, in combination with the presence of the basal cell spot and the straight median band on the underside of the hind wing and the usual presence of median spot 6 on the upperside of the hind wing, will usually suffice to identify this species. See also *zebra* and *sataspes*. In doubtful cases a genital examination is necessary, but this will seldom be the case.

Part of the literature suggests difficulties in distinguishing between *depauperata* and *diomus ferax* and, actually, *depauperata* was originally described as a "variety" of *"Hesperia ferax"*. There will be no problems if one pays attention to the following points:

1. on the upperside of both fore and hind wing the basal cell spots are absent (at most indicated by a few white scales) in *depauperata*, well-developed in *diomus ferax*.
2. on the upperside of the fore wing only one of the outer median spots in space 1b (viz., spot 1c) is present in *depauperata*, sometimes scarcely visible; in *diomus ferax*, both outer median spots are present and form a bar from vein 1 to vein 2.
3. on the underside of the hind wing the series of submarginal spots starts at the end of vein 7 in *depauperata*, at the end of vein 8 in *diomus ferax;* the distal edge of the median band reaches the termen at the end of vein 8 in *depauperata*, but crosses vein 8 well before its end and runs to the costa in *diomus ferax*.

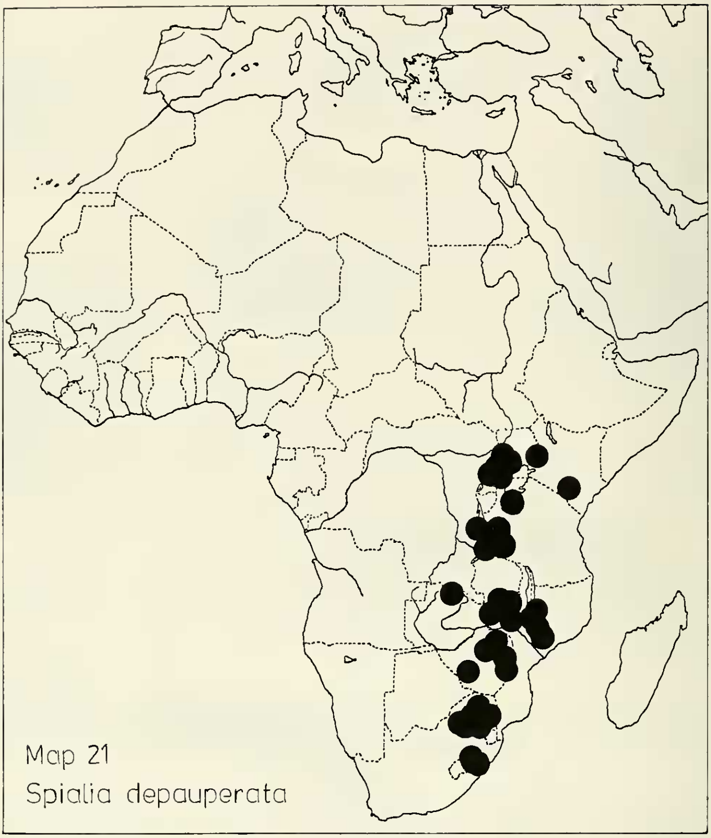
For variation, see subspecies.

Male genitalia (figs. 110, 111). — Uncus with high, longitudinal keel, apex usually more or less inflated. Relatively small fenestrula at junction of uncus and tegumen. Gnathos dorsally fused to tegumen, dorso-distal edge protruding; ventral part of gnathos somewhat more strongly sclerotized and with small, thick spines. Fultura superior smooth, passing into dorsal sclerotization of anellus. This sclerotization curves inward to form a shallow sac, and from there it extends as two strongly sclerotized and spined, oblong processes with a pointed apex on either side of the aedeagus. Aedeagus slightly bent in the middle, coecum shorter than wide, ventral process relatively small, somewhat longer than wide. Costa of valva expands distally and bears a twofold costal process. Distal part of costal process much as in *sataspes*, with radiating spines, but better developed; proximal part very heavily sclerotized, with serrated edge. Cucullus broadly developed, dorsally excavated to receive the costal process.



Figs. 112—116. Female genitalia, lateral and ventral aspect, and papilla analis. 112—114, *S. sataspes* (S. Africa). 115—116, *S. depauperata australis* (Muden, Natal).

Female genitalia (figs. 115, 116). — Ventral sclerites of segment 8 fused to a single sclerite. No antevaginal sclerotization. Postvaginally a narrow, V-shaped, membranous strip, flanked by slightly protruding sclerotization. Laterally some conspicuous, sclerotized folds. Distal edge of segment 8 straight. Papilla analis



rounded, nearly as long as broad; apophysis posterior slightly curving, about as long as papilla.

Ecology. — Mainly found on grassy hill-sides, where the skippers feed on flowers, but also found in the thorn bush. In S. Africa it is on the wing from July to April in two generations (Swanepoel, 1953). This may also be the case in the northern part of the range, but from there I have also seen specimens captured in May and June. Food plants have not been recorded.

Distribution (Map 21). — From Uganda and Kenya through eastern Africa south to Transvaal and Natal.

Geographic variation. — The width of the median band on the underside of the hind wing varies geographically, the northern populations showing a broader band. There is also some variation in the length of fore wing and the ground colour of the underside of the hind wing, but much overlap exists in these characters.

Spialia depauperata depauperata (Strand)

Hesperia ferax var. *depauperata* Strand, 1911. — Mitt. zool. Mus. Berlin 5 : 304 (Msamwia, between Lake Rukwa and Lake Tanganyika, S. Tanzania; not Msamusia, as stated by Evans, 1937). Holotype (♂) in the Zoologisches Museum der Humboldt-Universität, Berlin (labelled: S. Tanganyika, S. Ufipa, 25.1.09, Fromm.).

Syrichthus rehfousi Oberthür, 1912. — Ét. Lép. Comp. 6 : 117, fig. 1331 (Mpala, W. shore of Lake Tanganyika). Holotype (♂) in the British Museum (Nat. Hist.), London.

For the use of the name *abscondita* (see Evans, 1937) instead of *depauperata*, see synonymy of *diomus ferax*.

External characters (pl. 7 figs. 55, 56). — Median band on underside of hind wing broad, median spots 4—5 broader than width of ground colour in cell and usually also broader than width of ground colour between median and submarginal spots in spaces 4—5. This ground colour usually with a greenish tinge. ♂ (10.4—) 11.3—13.8 mm; the largest specimens are found in Malawi and S. Tanzania.

Distribution. — The northern part of the range, Uganda and Kenya southward to Zambia and Mozambique.

Localities. — Kenya: Kibwezi, Menfort, Mt. Elgon (BM, MN). Uganda: Ankole-Toro Border, SE. Ankole, W. Ankole, Kampala, Kafu R. nr. Hoima-Kampala Rd, Mbarara (S. Toro), Mulange (Mabira Forest), betw. Sezibwa R. and Kampala, Simba (W. Lake Victoria) (AMNH, BM). Tanzania: Geita, Mpanda, Ngamo, Ufipa, Wanzizi (BM, ML, MN). Zaïre: Ditanto, Marungu Plateau, Mpala (= Makowiri), Panda (BM, MRAC). Malawi: S. of Mangoche Mtn, Mlanje, Ncheu (BM, NMB; Gifford, 1965). Zambia: Petauke, Solwezi (BM, HDE; Neave, 1910, as *zebra*). Mozambique: Kola Valley, Tete to Ft. Jameson (Makanga Distr.) (BM, HDE; Neave, 1910, as *zebra*).

Material examined. — 45 ♂, 9 ♀ : 4 ♂, Kenya (BM, MN); 11 ♂, 1 ♀, Uganda (AMNH, BM); 14 ♂, 4 ♀, Tanzania (BM, ML, MN); 4 ♂ (incl. holotype *rehfousi*), Zaïre (BM, MRAC); 3 ♂, 1 ♀, Zambia (BM, HDE); 6 ♂, 3 ♀, Malawi (BM); 3 ♂, Mozambique (BM, HDE).

Spialia depauperata australis subspec. nova

Holotype (♀): Muden (Natal), 15.III.1948. British Museum (Nat. Hist.), London.

External characters. — Median band on underside of hind wing narrow, median spots 4—5 practically always narrower than width of ground colour in cell and between median and submarginal spots in spaces 4—5. This ground colour usually with a brownish tinge. ♂ 10.8—12.9 mm.

Distribution. — Transvaal and Natal, northwards probably to the Zambezi River.

Localities. — Rhodesia: Hunyani R. (Salisbury), Mtoko, Penkridge (Melsetter), Redbank (W. Matabeleland), Umtali, Vumba (BM, MN, NMB). South Africa. Natal: Estcourt, Ladysmith, Muden, Tugela, Weenen (BM, MN; Swanepoel, 1953). Transvaal: Letaba, Lydenburg, Munnik, Pietersburg, Potgietersrust, Warmbaths, Zoutpansberg (Swanepoel, 1953).

Material examined. — 44 ♂, 21 ♀ : 2 ♂, 1 ♀, Rhodesia (BM, MN). 42 ♂, 20 ♀ (incl. holotype), Natal (BM, MN, MRAC).

4. PHYLOGENY

Introduction

As said in the introduction to Chapter 3, the species groups recognized in this paper are thought to be monophyletic groups. Such a statement would have little value, if it was not accompanied by arguments. The argument for considering a group monophyletic (in the sense of Hennig, 1966) can only be the presence of an autapomorphy. Thus, in this chapter we shall investigate phylogenetically the various states of characters found in *Spialia* to find the arguments for the classification proposed in the previous chapter.

In a future paper I shall show that only few of the many arguments used in the literature to distinguish between plesiomorphous and apomorphous character states and to find monophyletic groups are supported by the evolutionary theory. Our present knowledge of *Spialia* allows the application of only three of these arguments, viz., (1) the argument of outgroup occurrence, (2) the argument of differentiation (complexity), and (3) the argument of vicariance. These arguments can be defined as follows:

(1) If in a monophyletic group a character occurs in more than one state, the state occurring also outside the group is considered plesiomorphous.

(2) If in a monophyletic group a phenocline of increasing differentiation or complexity can be distinguished, the evolution is supposed to have taken place in the direction of the strongest differentiation or the highest complexity, unless there are indications that reduction took place as a result of a particular mode of life.

(3) If in a monophyletic group of three or more species two species are vicarious, these species form a monophyletic subgroup (i.e. they are more closely related to each other than to any other species).

In the following lines these arguments will be applied to a number of characters. The outgroup is formed by the genera which are thought to be closely related to *Spialia*, viz., *Carcharodus, Gomalia, Celotes, Alenia, Syrichtus, Pyrgus* and *Heliopetes*. These genera, together with *Spialia*, are known as the *Pyrgus* group. Where appropriate, the outgroup will be extended to cover the whole subfamily Pyrginae or the whole family Hesperiidae.

In general the absence of a character in different species will not be taken as an indication of kinship relationship. This is based on the following reasoning. If a character arises, it can develop in a number of ways, each leading to a different type and representing a different evolutionary line, that theoretically can be traced back. A character can also be lost in different ways, each way representing a different evolutionary line, but as the result is the same in each way (loss of the character), the different evolutionary lines cannot be traced back.

Characters and character states

1. Wing markings

1.1. The central spot on the upperside of the fore wing is placed over or beyond the origin of vein 3 in *asterodia, agylla* and *kituina*, and before the origin of vein 3 in all other species of *Spialia*. The first condition is also found in *Syrichtus*, the latter in *Pyrgus*. So there is no clue to which condition is apomorphous and which plesiomorphous.

1.2. On the upperside of the fore wing there are no spots in spaces 9 and 10, except in *asterodia, agylla* and *kituina*. These spots are absent in the outgroup, except in *Pyrgus* and *Heliotepes*. In some *Syrichtus* species (*antonia, cribrellum*) the spots may be vaguely outlined. Also in a number of other genera of the subfamily Pyrginae there are spots in spaces 9 and 10. So there is no reason to consider the presence of these spots in some *Spialia* species otherwise than a plesiomorphous state. As said above, the absence of a character will not be considered proof of kinship relationship. Consequently, this character is not very well suited for our purpose.

1.3. The submarginal spots of the hind wing are in line, at equal distance from the termen, in all *Spialia* species except *colotes* and *confusa*, where the submarginal spots in spaces 4 and 5 are placed more basad. In the outgroup such a displacement is only found in various degrees in some *Syrichtus* species. As it may even vary within the species of *Syrichtus (poggei)*, the presence of this character state in *Syrichtus* and *Spialia* seems to be due to the phenomenon known as the Law of Vavilov (cf. Vavilov, 1922), rather than to autapomorphy. Therefore, in *Spialia* the shift of the submarginal spots in spaces 4 and 5 towards the base can be considered apomorphous.

1.4. In the *Pyrgus* group the basal spots on the underside of the hind wing are always detached from the median spots, except in two *Spialia* species, viz., *phlomidis* and *kituina*. In *phlomidis* it is the median band that bends to the basal spot in space 7, in *kituina* it is the basal spot in space 7 that is elongated towards the central spot of the median band. These unique arrangements of the spots can only be considered apomorphous states that originated independently. Considering one of these arrangements plesiomorphous would force us to recognize a large number of parallel changes in the arrangements of the spots, viz., towards a disconnection of basal and median spots. Only if the connection of basal and median spots was also found outside the *Pyrgus* group, there could have been a reason for considering the disconnection apomorphous.

1.5. In two *Spialia* species, viz., *spio* and *diomus*, a spot occurs between the median spot and the submarginal spot in space 1c on the underside of the hind wing. The spot does not occur in other species of the *Pyrgus* group and for that reason its presence is considered apomorphous.

2. Legs

2.1. In all *Spialia* species the mesotibiae are unspined, except for the two terminal spines, but in *diomus* the mesotibiae are provided with a double row of spines. In the outgroup this character is only found in *Syrichtus cribrellum*. It is possible that this is the result of common ancestry, in which case the spined mesotibiae constitute the plesiomorphous state in *Spialia*, unless we assume that *cribrellum* is a descendant of *diomus*. There is no ground for the latter assumption. The alternative explanation is a parallel development. Knowledge about the function of the spines could support this explanation. Unfortunately, we do not have the slightest idea of their function. At the moment this character can be used in phylogenetic considerations only in connection with other characters.

3. Secondary sexual characters

3.1. A costal fold in the fore wing, with specialized scales, is present in the males of five *Spialia* species, viz. *asterodia, agylla, kituina, colotes,* and *confusa.* In the outgroup a costal fold is absent in *Alenia,* one species of *Syrichtus* and a few species of *Pyrgus.* The character appears to be a characteristic of the subfamily Pyrginae, though it is absent in many species. Its intricacy suggests that it is an autapomorphy of the Pyrginae, that was lost independently in many cases. Thus the presence of a costal fold is considered here a plesiomorphy of *Spialia.*

Table 1. Families of food plants of *Spialia* species.

	Malvaceae	Sterculiaceae	Tiliaceae	Convolvulaceae	Rosaceae	unknown
asterodia	X	X				
agylla	X	X				
kituina						X
spio	X	X				
diomus	X	X				
phlomidis				X		
osthelderi						X
geron						X
doris				X		
colotes						X
confusa		X	X			
sertorius					X	
orbifer					X	
mafa	X					
galba	X	X				
wrefordi						X
paula						X
secessus						X
dromus			X			
ploetzi						X
mangana						X
nanus	X	X				
delagoae						X
zebra		X				
sataspes	X	X				
depauperata						X

Table 2. Families of food plants of the genera of the *Pyrgus* group. The Sterculiaceae and Tiliaceae, food plants of a number of *Spialia* species and closely related to the Malvaceae, have been omitted (see table 1).

	Malvaceae	Rosaceae	Convolvulaceae	Labiatae	Cistaceae	Acanthaceae
Celotes	X					
Carcharodus	X			X		
Gomalia	X					
Alenia						X
Syrichtus				X		
Spialia	X	X	X			
Pyrgus	X	X			X	
Heliopetes	X					

4. Ecology

4.1. All species of *Spialia,* as all species of the outgroup, are at home in open formations, though they may penetrate forests along paths, etc. There is only one exception, viz., *ploetzi.* This species is confined to the lowland evergreen forest. On the basis of outgroup comparison this habitat preference is considered apomorphous.

4.2. The food plants of Hesperiidae are only very incompletely known, but the little that is known appears to be interesting. Table 1 summarizes the families of the food plants of the *Spialia* species as far as known and table 2 gives the families of the food plants per genus of the *Pyrgus* group. From these tables it appears that the Malvaceae are the original food plant family of the *Pyrgus* group, as species of this family are used as food by species of almost all genera of the *Pyrgus* group. This idea is supported by the fact that Malvaceae are food plants of small and divergent genera like *Gomalia, Celotes* and *Alenia.* The divergence of these genera suggests that they departed since long from their common ancestor. It is very unlikely that they all independently adopted Malvaceae as food plants.

The *Spialia* species feeding upon Malvaceae usually also feed upon Sterculiaceae. These families are closely related and together with the Tiliaceae and some other families they form the order Malvales. As the food plants are incompletely known, the order Malvales instead of the family Malvaceae is considered here to contain the original food plants of the *Pyrgus* group (and of *Spialia*). It follows that the adaptation to Convolvulaceae and Rosaceae by some *Spialia* species is an apomorphous character state.

5. Male genitalia

5.1. A fenestrula is present in nine *Spialia* species, viz., *spio, mafa, galba, mangana, nanus, delagoae, sataspes, zebra* and *depauperata*. In the outgroup it is only found in *Syrichtus cribrellum*. This suggests that the presence of this character is an apomorphy in the *Pyrgus* group and a plesiomorphy in *Spialia*. However, a fenestrula occurs erratically outside the *Pyrgus* group, even in the subfamily Hesperiinae. Thus it may be an apomorphous state in the Hesperiidae that was secondarily lost on many occasions independently. The alternative explanation implies a parallel development (e.g. due to the Law of Vavilov). However it may be, the species of the *Pyrgus* group are all very similar, so that the idea that they are closely related, seems a good working hypothesis. If in such a group of species a character occurs in only few species, the presence of that character in these species seems to be due to common ancestry rather than to parallelism. This may be interesting for the relationship between *Syrichtus* and *Spialia*, but it implies that the presence of a fenestrula in *Spialia* is a plesiomorphous state that is of little use in the reconstruction of the phylogeny.

Though the presence of a fenestrula may have little value for the present study, its further development may be useful. In *Spialia galba* and *mafa*, namely, the fenestrula is very large, much larger than in any other species of the *Pyrgus* group. Therefore this excessive development of the fenestrula is considered apomorphous.

5.2. The uncus of the Hesperiidae exhibits a great variety of shapes and dimensions. In four *Spialia* species, viz., *delagoae, zebra, sataspes* and *depauperata*, the apex is inflated. This character does not occur in any other species of the *Pyrgus* group, nor in any other Hesperiid species examined by me. Therefore, I consider the presence of this character the apomorphous state.

5.3. An indented or bipartite uncus occurs in many Hesperiidae, in the Pyrginae as well as in the Hesperiinae. The same genus may have species with an entire and with a bipartite uncus, e.g. *Celaenorrhinus, Pyrgus*. Both types of uncus may even occur with a single species (*Pyrgus malvae*, see De Jong, 1972). The partition is very variable, suggesting that it arose several times independently. In *Spialia* two types of indentation occur:

1. in *asterodia, agylla* and *kituina* the uncus is bipartite, the two parts lying more or less parallel. This is a usual type in the *Pyrgus* group, being found in *Pyrgus, Heliopetes* and *Celotes*, though the parts are not always parallel. At the moment there is no reason not to consider this type an apomorphous state within the *Pyrgus* group, and thus a plesiomorphous state in *Spialia;*
2. in *zebra* the uncus is shallowly indented and the two parts are widely diverging, giving the uncus the shape of a Y or T. This type is unique and must be considered an apomorphous state.

5.4. There is a keel running dorso-centrally over the uncus in five *Spialia* species, viz., *nanus, delagoae, zebra, sataspes* and *depauperata*. This character is absent in all other species of *Spialia* and the other genera of the *Pyrgus* group. Therefore, its presence is considered to represent the apomorphous state.

5.5. The gnathos occurs in very different types in the Hesperiidae. Warren (1957), studying the gnathos ("lateral apophyses") of *Pyrgus* species, thought it to be the original tenth abdominal segment with sclerites of the twelfth segment, but his argumentation is little convincing. I very much doubt if the gnathos is homologous in all Lepidoptera where it occurs. If a gnathos is developed to some extent, it appears to have a distinct function, being an extra grip during copulation. As it apparently has adaptive value, it may be expected that adaptive radiation has occurred and that more or less similar types originated more than once from the same basic structure.

Confining ourselves to the *Pyrgus* group, the following phenocline can be observed:

a. sclerotization of fultura superior from right and left sides of tegumen downwards (towards aedeagus sheath);

b. differentiation of ventral parts of downward sclerotizations (sclerotization stronger and better defined, development of spines, etc.);

c. sclerotization gets detached from tegumen (greater freedom of movement).

Stage c occurs only in conjunction with stage b. Applying the argument of differentiation the phenocline can be read phylogenetically in the direction a → b → c. Reading it in the reverse direction would imply that from a great variety of forms (and how would they have originated?) reduction took place to a slight sclerotization of the fultura superior and eventually to a fusion of this sclerotization with the tegumen. Such a development would make little sense and is difficult to understand.

In *Spialia* the following types are found:

1. stage a: *colotes, confusa, paula, wrefordi, secessus, dromus, ploetzi;*
2. stage b: 1. ventral parts strongly sclerotized but smooth: *asterodia, agylla, kituina;* 2. ventral parts spined, no definite protrusions, dorsal parts broad: *sataspes, depauperata;*
3. stage c: 1. ventral parts spined but no definite protrusions ("heads"): *spio, diomus, mangana, zebra, nanus;* 2. ventral parts forming definite, spined protrusions ("heads"): *phlomidis, osthelderi, geron, doris, galba, mafa, sertorius, orbifer, delagoae.*

5.6. In some species of the *Pyrgus* group the fultura superior is densely set with long, but weak spines (sometimes more looking like hairs), especially in the medioventral part. This is found in a number of species of *Syrichtus* and *Spialia*, so that it appears that it is a plesiomorphous state in *Spialia*. It is usually found in conjunction with gnathos stage a, suggesting that it has the same function as the spined heads of the gnathos found in stage b. The extension of the spines varies from an undefined area to a well-defined area covering two semiglobular membranous folds in the ventral part of the fultura superior, in connection with the rather undefined gnathos. As the latter situation is a further differentiation, it is supposed here to be apomorphous. It is found in *paula, wrefordi, secessus, dromus* and *ploetzi,* and to some extent in *mangana.*

5.7. In some *Spialia* species sclerotization occurs in the dorsal parts of the aedeagus sheath. This is unusual in the *Pyrgus* group. As the sclerotization is a further differentiation and the two types of sclerotization found in *Spialia* do not occur in the outgroup, they are supposed to have originated independently from the unsclerotized stage. The two types are:

1. rather well defined sclerite dorsally over aedeagus. This sclerite is not flat, but gutter-like (*wrefordi, secessus, dromus, colotes, confusa*) or roof-like (*paula, ploetzi*). The relationship between these subtypes is not clear at the moment and they are considered as belonging to the same type till more can be said about their relationship;
2. dorso-laterally, to the right and to the left, a strongly sclerotized and spined protuberance; the aedeagus sheath membrane between the right and left parts more or less strongly sclerotized. This is found in *mangana, nanus, delagoae, zebra, sataspes,* and *depauperata*. This type looks like a further differentiation of the first type. Support for this suggestion must be looked for in the distribution of other characters.

5.8. In the *Pyrgus* group the surface of the aedeagus is smooth or at most with fine spines, except in some *Spialia* species. According to the argument of outgroup comparison, the presence of outgrowths in *Spialia* is apomorphous. Three types are found:

1. *delagoae* type — a short, ventral cylindrical, spined excrescence: *mangana, nanus, delagoae, zebra, sataspes, depauperata;*
2. *phlomidis* type — a lateroventral, strongly sclerotized, dentate ridge: *phlomidis, osthelderi, doris;*
3. *geron* type — a lateroventral, long, cylindrical, smooth excrescence, giving the aedeagus a forked appearance: *geron.*

The *phlomidis* and *geron* types look dissimilar, except that the position of the excrescence (to the left) is identical. However, all other characters (see, e.g. the female genitalia, below) point to a close relationship of the species exhibiting these types of aedeagus and for that reason the long excrescence of the *geron* type of aedeagus is considered here a further differentiation of the *phlomidis* type (see also De Jong, 1974).

The *delagoae* type appears to be a development that is quite independent from the other types. It is, indeed, difficult to imagine a relationship between these types, not only the form but even the position of the outgrowth being dissimilar. In view of the present knowledge we can only consider the *delagoae* type an independent line of evolution.

5.9. In all species of the *Pyrgus* group the aedeagus is straight or very slightly bent, except in the *Spialia* species *wrefordi* and *ploetzi,* where it is clearly bent to a more or less S-shaped structure. Because of its distribution in the *Pyrgus* group the bent condition is considered apomorphous.

5.10. In all species of the *Pyrgus* group the aedeagus has a well-defined coecum, except in a number of *Spialia* species, where the coecum is shortened. These species are: *delagoae, nanus, zebra, sataspes, depauperata,* and *mangana.* In the last species the coecum is practically lost. As the differences in length of the coecum between the species are often very slight, an arrangement of the species in a phenocline would be rather arbitrary, except for the extreme condition found in *mangana.*

Because of the state of this character in the outgroup, the tendency to shorten the coecum must be considered apomorphous.

5.11. The valvae have a clear function during copulation: they clasp the end of the female abdomen. For a better grip the inside is often provided with prominent outgrowths, spines, haires, etc. This is the general picture throughout the Lepidoptera. Often various types of ornamentation of the inside of the valvae can be found within a group of genera or even within a genus. So three types can be found in *Spialia,* all referring to the differentiation of the costa:

1. *phlomidis* type — distal end of costa more or less widened, ventrally usually with a strongly spined outgrowth or dorsally with a finger-like excrescence: *phlomidis, geron, osthelderi, doris, spio, diomus;*
2. *kituina* type — ventro-distally a heavily sclerotized appendix with at least two heavy spines: *asterodia, agylla, kituina;*
3. *sertorius* type — ventro-distally a more or less differentiated appendix that is not more heavily sclerotized than the remainder of the costa and bears long, relatively soft spines: remainder of *Spialia.*

The *kituina* and *sertorius* types are sufficiently differentiated to consider them to represent two different, independent evolutionary lines: they are so much complicated that a single origin of each of both types can be accepted and they differ so much that a development of one type into the other is difficult to imagine. As these types are unique in the Hesperiidae, they are both considered apomorphous, but it is not easy to find the respective sister groups with the plesiomorphous state. The *phlomidis* type is rather varied and relatively simple. It comes closest to what is found in the other genera of the *Pyrgus* group, especially *Syrichtus* and *Carcharodus.* For this reason it is supposed to have departed not far from the ancestral type of *Spialia.* It is too varied to be simply considered the plesiomorphous state of one or both of the other types. The species, however, with this type of costal development can, as a group, quite well be considered the sister group of the group of species exhibiting one of the other types.

5.12. Within the *kituina* and *sertorius* types mentioned in 5.11. a phenocline of increasing complexity can be observed. As the primitive state of these types is supposed to have been rather simple (see above) and there is no reason to suppose that reduction took place (that would even be inconceivable in the *kituina* type, see below), the phenoclines may represent phyloclines. The clines are as follows:

1. *kituina* type — a. costa smooth (except for costal process), costal process relatively little differentiated (*asterodia*); b. costa with some short spines, costal process more differentiated (*agylla*); c. costa with some short spines, costal process gets loose from costa and joins cucullus (*kituina*). If *asterodia* had developed its costal process from the type found in *kituina,* i.e. through reduction of the costal process of *kituina,* then the latter would have rejoined the costa before further reduction, an inconceivable development. As the costal process in *kituina* cannot be said to be more differentiated than that in *agylla* (it is only dissimilar and has another position), it is quite well possible to suppose that *kituina* arose from an *asterodia*-like ancestor, independent from *agylla.* In that case the spines on the costa in *kituina* and *agylla* represent a parallel development.

2. *sertorius* type — a. costal process relatively small, rounded, with spines radiating to the ventral side (*mangana, zebra, sataspes, depauperata*); b. costal process elongate towards base of valva, spines radiating to the ventral side, but spines directed to the base of the valva predominant (*wrefordi*); c. costal process elongated, straight or curved upwards, all spines directed to the base of the valva (*paula, secessus, dromus, ploetzi, nanus, delagoae*). Starting from a), a second phenocline of the *sertorius* type of costal process can be observed, in which the connection between the costal process and the costa narrows, so that the costal process looks more separate, while the spines are not radiating, but directed basad and distad (*colotes, confusa*) or distad only (*sertorius, orbifer, mafa, galba*). As both phenoclines show an increasing differentiation, they are considered to represent phyloclines.

5.13. There are some further developments of the costa, which for their uniqueness in the *Pyrgus* group are considered apomorphous. They are:

1. In *ploetzi* the costa is extended distally over the cucullus.
2. In *confusa* the costa has grown fold-like over the costal process.
3. In *osthelderi, geron* and *doris* the costa is spined dorsally.

5.14. The cucullus is far less differentiated than the costa in *Spialia*. There are only two remarkable differentiations:

1. In the species with a costal process, except in *mangana, nanus, delagoae, zebra, sataspes* and *depauperata*, the cucullus is extended at the inside into a thin fold that more or less covers the costal process. Outside *Spialia* a cucullus fold occurs only in *Carcharodus alceae*, be it in another form. As *C. alceae* is in all other aspects very different from *Spialia*, the common possession of a cucullus fold is supposed to be a parallelism. Not only for the outgroup comparison, but also for the fact, that the cucullus fold appears to be correlated with the costal process, the presence of the fold is considered apomorphous. It would be interesting to know the function of the fold. If the costal process has developed as an extra grip during copulation, the cucullus fold must again reduce its effect.
2. In *doris* the cucullus is divided into two parts, apparently an apomorphous condition as it is a further differentiation of the cucullus, that does not occur elsewhere in the *Pyrgus* group. The division of the cucullus found in some members of *Syrichtus* is of another type (see a forthcoming paper on the genera of the *Pyrgus* group).

6. Female genitalia

6.1. The eighth abdominal segment is strongly modified in connection with the genitalia, especially the ventral part. The dorsal part is much less modified and in *Spialia* we can distinguish between two different types of sclerotization, viz., a) a single sclerite (tergite) covering the greater part of the dorsal area (*asterodia, agylla, kituina*), and b) two smaller sclerites, mid-dorsally separated by a membranous area (all other *Spialia* species). The first type is found in the outgroup in *Carcharodus, Celotes* and *Alenia*, and also outside the outgroup (e.g. *Erynnis, Xenophanes, Lobocla*). For this reason, and because a single tergite most closely corresponds with what must have been the original shape of the eighth tergite in females, the first type is considered plesiomorphous.

6.2. The dorsal sclerites of the eighth abdominal segment are never fused to the ventral sclerites in the *Pyrgus* group, except in the *Spialia* species *sertorius, orbifer, mafa,* and *galba,* while in *colotes* and *confusa* the dorsal and ventral sclerites practically touch. Thus, in *Spialia* there is a phenocline in the fusion of the dorsal and ventral sclerites, with three stages, viz., a. not fused; b. touching; c. fused. As the first stage is the usual one in the *Pyrgus* group (and outside), the phenocline a → c is supposed to represent a phylocline in the same direction.

6.3. The development of the ventral sclerites of the eighth abdominal segment is too varied to discover a certain line of evolution in it. If, e.g., the ventral sclerites are fused postvaginally, it cannot be determined whether this is due to extension of the sclerites or to an extending sclerotization of the postvaginal membrane. Therefore, the characters of the ventral sclerites are left out of consideration here (see, however, the discussion of the *delagoae* group).

6.4. In a number of *Spialia* species there is a distinct area spinulosa, viz., *spio, diomus, colotes, mafa, galba, sertorius, orbifer, wrefordi, paula, secessus, dromus,* and *ploetzi,* and in a few others there may be some indistinct spines postvaginally. An area spinulosa is also found in the outgroup, in *Syrichtus* and *Carcharodus.* Therefore I consider its presence a plesiomorphous condition. With increasing sclerotization of the postvaginal area the spines seem to tend to disappear. As the sclerotization probably evolved along different lines (see 6.3.), the absence of spines in different species is not necessarily an autapomorphy.

6.5. A unique development in the *Pyrgus* group, and probably outside as well, is the presence of strongly sclerotized, serrated "wings" at the proximal edge of the ventral side of the eighth abdominal segment in the *Spialia* species *phlomidis, osthelderi, geron, doris, spio,* and *diomus.* In the last two species there is only a weak development of these structures. Thus, there is a phenocline as follows: a. no "wings"; b. small, indistinct "wings"; and c. large "wings". In view of the absence of these structures outside *Spialia* their presence is supposed to be apomorphous and the phenocline is considered to represent a phylocline in the direction a → c.

6.6. In two *Spialia* species, viz. *spio* and *diomus,* the postvaginal area is provided with a tongue-like outgrowth that partly covers the area spinulosa. Outside *Spialia* a similar structure is only found in *Carcharodus lavatherae.* For the rest, *C. lavatherae* and the *Spialia* species are so dissimilar that it seems most plausible, that the outgrowth arose independently in *Carcharodus* and *Spialia,* just as sclerotization in the same area must have arisen more than once. Consequently, the presence of this outgrowth in *Spialia* is considered apomorphous.

6.7. The ductus bursae is smooth and more or less straight in all species of the *Pyrgus* group, except in two *Spialia* species, viz., *colotes* and *confusa,* where it is distinctly bent shortly before the bursa; the wall is corrugated at this place. In view of the distribution of this character its presence is considered the apomorphous condition.

6.8. In all species of the *Pyrgus* group the bursa copulatrix is without ornamentation, except for *Spialia galba,* which has a large, finely spined area in the bursa. Apparently an apomorphous character state.

6.9. Ten *Spialia* species have a basal lobe on the papilla analis. In the *Pyrgus*

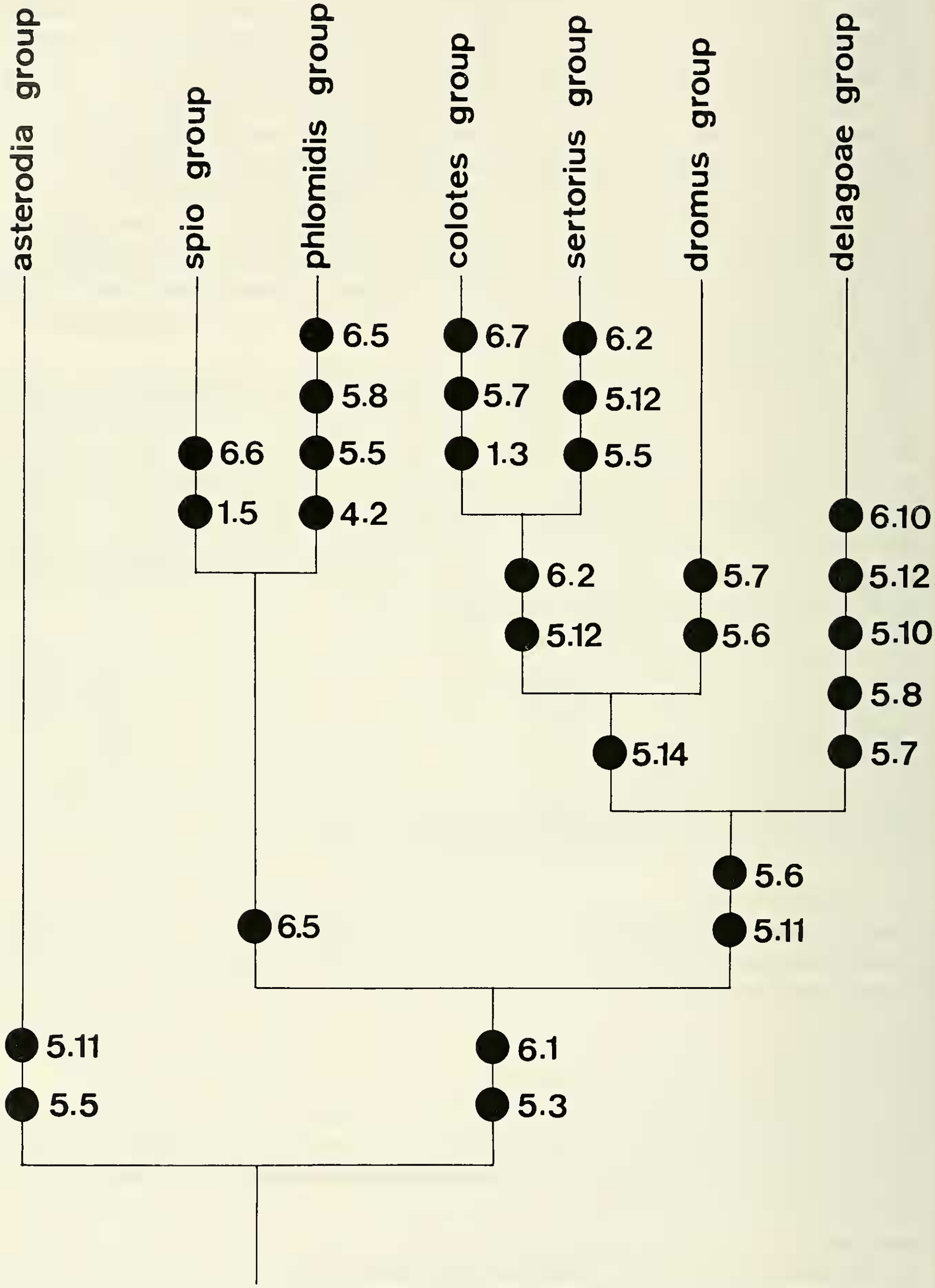


Fig. 117. Supposed evolution of *Spialia*. Black dots indicate apomorphous character conditions, the plesiomorphous condition of the same characters is supposed to be present in the sister groups. The numbers refer to the paragraphs in the text where the relevant characters are discussed.

group a basal lobe is further found in *Carcharodus* (one species only), *Alenia* and *Syrichtus*. If the presence of a basal lobe is not plesiomorphous in *Spialia*, then the structure arose so often independently that it is of little use for phylogenetical considerations.

6.10. Although the papillae anales are variously shaped in the *Pyrgus* group and for that reason are difficult to interpret phylogenetically, an exception must be made for the remarkably shaped papillae anales of the *Spialia* species *mangana, nanus, delagoae, zebra, sataspes,* and *depauperata,* with their short and broad body, and short, curved apophyses posteriores, giving the appearance of a quite distinct type of structure. I cannot do otherwise than considering this type apomorphous in relation to the type found in the other *Spialia* species.

The above considerations are the arguments for the reconstruction of the phylogeny as shown in fig. 117. For the sake of surveyability the diagram has been drawn up to the level of the species groups recognized in this paper, to show the phylogenetic basis for the division into species groups. The further development will be dealt with below for each species group separately and further diagrams will be provided for the *dromus* and *delagoae* groups. For diagrams of the *phlomidis* and *sertorius* groups the reader may be referred to my earlier paper (De Jong, 1974). The other species groups consist of so few species that the diagrams would have no meaning at all.

The phylogeny of the species groups

The *asterodia* group

Starting from the supposed monophyly of *Spialia* (see Introduction and a future paper on the genera of the *Pyrgus* group) the remainder of *Spialia* is considered the sister group of the *asterodia* group. Autapomorphies of the latter are the smooth, well-defined, heavily sclerotized gnathos and the peculiar shape of the costal process of the valvae.

It is surprising that the characters by which the species can so easily be distinguished, viz., the position of the central cell spot on the upperside of the fore wing and the presence of a costal fold at the fore wing in the male, cannot on the basis of our present knowledge be considered autapomorphies of the group. By these characters and by the single eighth tergite of the female abdomen and the bipartite uncus in the male genitalia, the group stands out as having retained a relatively large proportion of primitive character states, though it has developed some pecularities of its own. In all, it gives the impression of a group of which the ancestor has departed since long from the main stem of *Spialia*.

The development of the group seems to have been greatly influenced by the division of the original distribution area into two parts. This resulted in two species in South Africa (*asterodia* and *agylla*) that are very similar, and one divergent species in East Africa (*kituina*). The close resemblance between *asterodia* and *agylla* suggests that they originated after the separation of the East African population. Autapomorphies of *kituina* are the position of the costal process of the valva and the peculiar Y-mark on the underside of the hind wing. For *asterodia* +

agylla no autapomorphies can be listed at the moment. See also the discussion under 5.12.

The sister group of the *asterodia* group

The monophyly of this group is based on two autapomorphies, viz., the undivided uncus of the male and the double tergites of the eighth abdominal segment of the female. If this is correct, the group must have had a relatively simply built valval costa, which only differentiated after the next cleavage of the phylogenetic line. This cleavage gave rise to the ancestor of both the *spio* and *phlomidis* groups and to the ancestor of the remainder of *Spialia*.

In the line leading to the *spio* and *phlomidis* groups the male genitalia remained relatively simple, the main differentiation affecting the gnathos, but a remarkable development took place in the female genitalia, viz., the development of antevaginal, free sclerotizations ("wings"). If such sclerotizations arose more than once in *Spialia,* it can hardly be assumed that they would be of the same type. Therefore, the monophyly of the *spio* + *phlomidis* group is considered rather well established, though based on a single autapomorphy.

In the line leading to the remainder of the genus the main development took place in the male genitalia, where the costa developed a special, spined structure, viz., the costal process, and the gnathos became increasingly differentiated. The costal process is basically so uniform in the different species, that it does not seem too risky to accept it as an autapomorphy of the four remaining species groups.

One may wonder if it is not significant that the development of the female genitalia in one line and of the male genitalia in the other both seem to serve a better grip during copulation. If this is true, then it is understandable that in different lines male and female genitalia evolve in an inversely proportional way. At the moment this is pure speculation, but it may point to an important field of research, viz., the exact use of the various parts of the genitalia during copulation.

The *spio* group

The species in this group, *spio* and *diomus,* are considered sister groups because of two apomorphies which are both supposed to have arisen only once, viz., the presence of a tongue-like postvaginal structure in the female and the presence of an extra spot between the median and submarginal spots in space 1c on the underside of the hind wing. Another shared character, which cannot however be called an apomorphy, is their almost pan-Afrotropical distribution. For the rest they are rather divergent, especially in the male genitalia, suggesting that their origin is not very recent. As the male genitalia of *spio* most closely resemble those of the sister group of the *spio* group, it appears that *diomus* has drifted farther away from the ancestral condition. This being so, the spines on the mesotibiae of *diomus* are rather a new development than a relic from ancient times.

This group is an example of the influence of phylogenetic considerations on classification. Higgins (1924) thought the differences in the wing markings too large to unite *spio* and *diomus* into a single group. Instead, he placed *mafa* and *paula* with *spio,* as these species lack the median spot 6 on the underside of the hind wing. As said before, absence of a character in different species should not be taken as an indication of kinship relationship, as loss of a character may easily occur more than once by different causes. Thus, the typologically based group *spio* + *mafa* + *paula* is replaced by the phylogenetically based group *spio* + *diomus*.

The *phlomidis* group

The monophyly of this group is well established by the shared possession of four apomorphies, viz., food plants (Convolvulaceae), differentiation of gnathos, ornamentation of aedeagus, and large, winged, antevaginal sclerotizations. The further development of the group was treated in an earlier paper (De Jong, 1974) and there is no need to repeat the discussion here.

The sister group of the *spio* + *phlomidis* group

It seems that after the first cleavage of this group two sister groups originated with highly different rates of evolutionary change. While the line giving rise to the *delagoae* group apparently only split further after having obtained a number of new character conditions, so that the species share a large number of apomorphies, the other line split already after a single new development, viz., an excavation of the dorsal part of the cucullus resulting in a fold that partly covers the costal process. As a result, the *colotes* + *sertorius* + *dromus* group looks less homogeneous than the *delagoae* group. This is, of course, not an unexpected statement, as the heterogeneity of the first group was the first reason for a division into three species groups; it only shows the evolutionary background of this arrangement. In fact the possession of a cucullus fold was not an entirely new development of the *colotes* + *sertorius* + *dromus* group. It apparently started with a hollowing of the dorsal part of the cucullus. This development must have started before the cleavage with the *delagoae* line was finished, as the excavation of the cucullus can also be seen in the *delagoae* group. But the character attained full development only in the other line (see, however, the discussion on the *sertorius* group).

After cleavage of the *colotes* + *sertorius* + *dromus* line the costal process of the valva, still a rather undifferentiated excrescence with spines, begins to contract to an oval shape in one of the sister groups, the *colotes* + *sertorius* group, while also a tendency develops for the dorsal and ventral sclerites of the eighth abdominal segment of the female to fuse. By these two new developments the monophyly of the *colotes* + *sertorius* group is rather well established. There is, however, one difficulty. If the reconstruction of the phylogeny given here is correct, then the dorsal sclerotization of the aedeagus sheath found in the *colotes* and *dromus* groups must have arisen twice. Making, for the sake of this character, the *colotes* + *dromus* group sister group of the *sertorius* group, would compel us to accept an independent development of the differentiation of the costal process and the tendency to fusion of the ventral and dorsal sclerites of the eighth abdominal segment of the female in the *colotes* and *sertorius* groups. Just one parallel development against two. I have thought it wisest to choose for parsimony here and to attribute the occurrence of sclerotization of the aedeagus sheath in two species groups to the Law of Vavilov.

Yet another character may seem to couple the *colotes* and *dromus* groups, viz., the spined fultura superior. In the *colotes* group, however, this character appears to exist in a primitive stage, much like the condition it must have had before the *dromus* group and even the *delagoae* group branched off, and different from the large semiglobular folds characteristic of the *dromus* group.

It may be remarked that the above reasoning were superfluous if the *colotes, sertorius* and *dromus* groups were united into one species group, as sister group of the *delagoae* group. This would, however, only have moved back the problems to the moment the development within the combined group had to be dealt with.

The *colotes* group

Leaving the dorsal sclerotization of the aedeagus sheath out of consideration, the monophyly of the group is sufficiently established by the corrugation and bend of the ductus bursae and the inward shift of the submarginal spots 4 and 5 of the hind wing. A diagnostic character of the group is further the presence of a costal fold at the fore wing in the male. However, as said before, this character has a very scattered distribution throughout the Pyrginae and the genetics ruling its development are not yet understood, making it worthless at the moment for phylogenetic studies.

The most remarkable new development within the group is the fold that from the costa of the valva extends over the costal process in *confusa*. However, as the group consists of only two species, *colotes* and *confusa,* the further development of the group is of little interest from the phylogenetic point of view.

The *sertorius* group

Autapomorphies of this group are in the male the differentiation of the ventral part of the gnathos into spined heads and the differentiation of the costal process with spines directed only distad, and in the female the fusion of the dorsal and ventral sclerites of the eighth abdominal segment. These apomorphies appear enough to establish the monophyly of the group firmly. It is therefore surprising to find that in two of the four species of the group, viz., *sertorius* and *orbifer,* the cucullus fold is not much developed, suggesting a rather primitive state of this character, dating from before the cleavage with the *delagoae* group. If on the ground of this character *sertorius* and *orbifer* were left out of the group and placed as a group that originated before or shortly after the cleavage that gave rise to the *delagoae* group, then all the autapomorphies of the "old" *sertorius* group, of the *sertorius* + *colotes* group and of the *colotes* + *sertorius* + *dromus* group were based on parallel developments and no true autapomorphies. It seems more plausible that the cucullus fold was reduced in *sertorius* and *orbifer,* as a secondary development.

The group falls apart into two apparently monophyletic groups, viz., 1. *sertorius* + *orbifer* — autapomorphies: larval food plants belong to Rosaceae, almost complete fusion of dorsal and ventral sclerites of eighth abdominal segment in the female;

2. *mafa* + *galba* — autapomorphy: very large fenestrula. The dorsal and

ventral sclerites of the eighth abdominal segment of the female are only partly fused, not over their whole length.

For further details on the development of the group (also subspecific) the reader is referred to De Jong (1974).

A remarkable feature of this group is the allopatry of all species (*sertorius* and *orbifer* may overlap to a small extent). This is partly due to colonization from Africa across the Saharo-Arabian eremic zone, which made a subsequent sympatry very difficult. This will be dealt with in the next chapter.

The *dromus* group

The autapomorphies of this group are found in the male genitalia: the large, semiglobular, spined folds of the fultura superior and the elongated costal process. The female genitalia do not yield characters that at the moment can be interpreted phylogenetically, with exception of the very deeply incised area spinulosa in *wrefordi*, a unique and for that reason supposedly apomorphous character state.

For the reconstruction of the phylogeny of the group the following characters can be used:

a. costal process — plesiomorphous: *wrefordi;* apomorphous: *paula, secessus, dromus, ploetzi* (see above, 5.12);

b. costa of valva — the distal end of the costa is usually rounded in *Spialia,* but in *secessus* and *dromus* it is more or less angulated, and in *ploetzi* it is elongated (see 5.13). This is a phenocline leading to an increasing differentiation and, for that reason, considered to represent a phylocline. In *paula* the dorsal ridge of the costa slopes gently down distally and the costa is only vaguely outlined ventrally;

c. area spinulosa — this part of the female genitalia shows some variation in the *Pyrgus* group, especially with regard to the distal rim being arched, straight or slightly indented. In view of this variation the situation in *wrefordi* (an almost bipartite area spinulosa) can only be considered apomorphous;

d. habitat preference — the only *Spialia* species (virtually the only species of the *Pyrgus* group) that is confined to the forest, is *ploetzi*. This preference is considered apomorphous (see 4.1);

e. seasonal dimorphism — although in species of the *Pyrgus* group with more than one generation per year the adults may vary seasonally, the dimorphism found in *secessus,* in which the white of the spots on the underside of the hind wing is entirely replaced by brown in the dry season, is unique. For this reason the dimorphism of *secessus* is considered apomorphous.

On the basis of these characters the reconstruction of the phylogeny of the group in fig. 118 has been made. The following comments may be added:

1. The aedeagus is distinctly bent in *wrefordi* and *ploetzi*. This was considered apomorphous (see 5.9.). On the basis of the other characters, however, we must conclude that it is a parallel development in these species.

2. The monophyly of *secessus* and *dromus* is not very well established, as it is not based on autapomorphies. Although these species have abundantly differ-

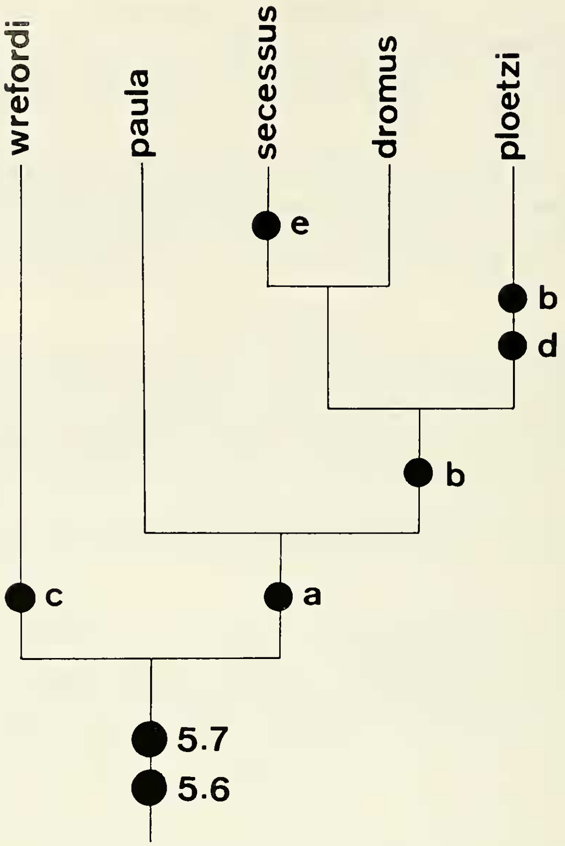


Fig. 118. Supposed evolution of the *Spialia dromus* group. Only apomorphous conditions have been indicated (see also fig. 117). Numbers and letters refer to the relevant paragraphs in the text.

ent wing markings, their male and female genitalia are much alike and on the basis of the present knowledge it cannot be stated whether this is due to symplesiomorphy or synapomorphy. At the moment the reconstruction of the phylogeny as given in fig. 118 seems the most probable one. It may be remarked that, if it turns out that the similarity of *secessus* and *dromus* is due to symplesiomorphy, this does not a priori imply that *secessus* and *dromus* are no sister groups.

The *delagoae* group

The species of this group share relatively many apomorphies, indicating that their ancestor had already departed far from the ancestor of the *colotes* + *sertorius* + *dromus* + *delagoae* group before it split further to the present situation. For the reconstruction of the phylogeny of the group the following apomorphous character states can be used:

a. apex of uncus more or less inflated: *nanus, delagoae, zebra, sataspes, depauperata* (in *nanus* more rounded than inflated) (see 5.2).

b. uncus bifid: *zebra* (see 5.3.).

c. uncus with a longitudinal, dorsal ridge: *nanus, delagoae, zebra, sataspes, depauperata* (see 5.4).

d. ventral differentiation of gnathos. The kind of gnathos found in the *delagoae* group is unique. There appears to be a phenocline of increasing differentiation from a *dromus*-like gnathos (*mangana*) through the ventrally still undifferentiated gnathos of *nanus* to a stronger differentiation in the ventral parts. Two types can be distinguished: 1. gnathos ventrally strongly sclerotized with some tubercles or short spines (*zebra, sataspes, depauperata*), and 2. gnathos ventrally with a strongly spined excrescence (*delagoae*). Both types may have arisen from the same undifferentiated *nanus*-like type.

e. costal process. The costal process occurs in two forms in the *delagoae* group, viz., as a rather undifferentiated outgrowth of the costa with radiating spines (*mangana, zebra, sataspes, depauperata*), and as an elongated excrescence of the costa, directed towards the base of the valva (*nanus, delagoae*). As explained in 5.12 the first type represents the plesiomorphous type. The simplest development of the costal process is found in *mangana*. In view of the occurrence of other plesiomorphous character states in *mangana* (gnathos, see above; female genitalia, see below), we may suppose that the simplicity of the costal process of *mangana* is not due to reduction, but represents a very primitive state. The elongated form of the costal process of *nanus* and *delagoae* reminds of the costal process of the *dromus* group. This can, however, only be due to convergence, unless all apomorphous characters shared by *nanus* and *delagoae* with the other species of the *delagoae* group, are due to convergence. Moreover, the costal process of *nanus* and *delagoae* extends from a very narrow, reduced costa, as in the other species of the *delagoae* group, and not from a well developed or even expanded costa as in the *dromus* group. Thus, the elongated costal process of *nanus* and *delagoae* is considered an apomorphous state.

A remarkable development is found in *depauperata:* apart from the usual costal process there is an extra, strongly sclerotized outgrowth with a serrated edge at the ventral side of the costa, close to the costal process. Such a unique development can only be considered apomorphous, no similar structures being known.

f. Under 6.3. it was stated that the sclerotization of the ventral side of the eighth abdominal segment of the female is too varied to be of use for phylogenetic considerations. An exception, however, must be made for the *delagoae* group. In all *Spialia* species (as in other species of the *Pyrgus* group) some part of the postvaginal area is membranous. In the *delagoae* group there is an increasing sclerotization of the postvaginal area, starting from a central sclerotization, as in *mangana* that fuses with the ventral sclerite, as in *nanus, delagoae, zebra* and *sataspes,* and leads to an almost entirely sclerotized ventral side of the eighth abdominal segment, as in *depauperata,* where the area spinulosa is entirely incorporated in the sclerotization and has lost its fine spines. In view of the development of the female genitalia in the other *Spialia* species and outside *Spialia,* the progressing sclerotization of the postvaginal area in the *delagoae* group must be considered to represent a progressing apomorphy.

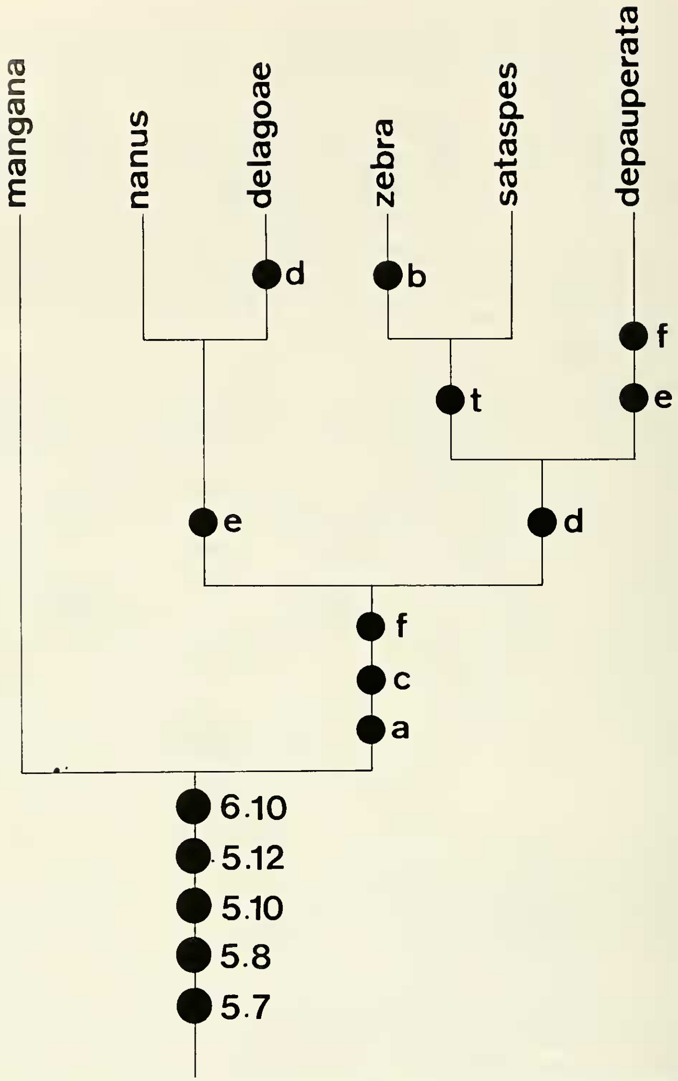


Fig. 119. Supposed evolution of the *Spialia delagoae* group. Only apomorphous conditions have been indicated (see also fig. 117). Numbers and letters refer to the relevant paragraphs in the text; t refers to the general discussion of the evolution of this group.

The reconstruction of the phylogeny of the group in fig. 119 is based on the above considerations. It may seem surprising that no apomorphies have been indicated for *mangana,* suggesting that this species has remained unchanged after the ancestor of the other species split off. This is improbable; there are several characters that in *mangana* undoubtedly occur in an apomorphous state, but this state becomes apparent only after *mangana* has been placed as sister group of the remainder of the *delagoae* group and, for that reason, cannot be used as argument for the drawing-up of the phylogeny. Such apomorphies are: 1. gnathos free from tegumen; 2. apex of aedeagus flattened and wide, spoon-like; 3. coecum virtually absent (see 5.10); 4. strong antevaginal sclerotization; 5. complete lack of submarginal spots on all wings.

Also the supposed monophyly of *zebra* and *sataspes* calls for explanation. It is difficult to give a single autapomorphous character state of these species. They are, however, so similar in a number of characters, that there is a fair chance that at least one of the characters occurs in an (aut-)apomorphous state in *zebra* and *sataspes*. Such characters are: 1. extension and shape of sclerotization in dorsal part of aedeagus sheath and in membrane between aedeagus sheath and gnathos; 2. short, slightly bent aedeagus; 3. short ventral process of aedeagus; 4. length of coecum; 5. apparent absence of cornuti; 6. general shape and development of valva. Further, if the monophyly of *zebra, sataspes* and *depauperata* is correct, the geographic vicariance of *zebra* and *sataspes* may be an indication of their close relationship, but the same applies to *sataspes* and *depauperata*.

5. GEOGRAPHIC HISTORY

As there are many factors that may influence the distribution history of a species, it is usually little rewarding to study the history of a single species if it is not possible to compare it with the history of the fauna the species belongs to. Thus in Europe, where the history of the fauna is relatively well-known, a study of the distribution history of a single species may yield some results. In tropical Africa, however, where the knowledge of the faunal history is extremely fragmentary, we can only hope to get some results by studying geographic patterns of distribution and evolution. A pattern, however, implies repetition and thus, it emerges only when many species can be compared. For that reason the genus *Spialia*, including only 26 species of which 20 occur in tropical Africa, does not seem an appropriate subject for a study of the geographic history. It appears, however, that even from the relatively few species a pattern of distribution and speciation arises that is worth discussing, as it may have some bearing on the general history of the fauna of open formations (the usual habitat of *Spialia* species).

Distribution patterns

In Chapter 4 it was supposed that the preference for forest in *Spialia ploetzi* is a recent development, coinciding with other recent developments in the same species. The other *Spialia* species have, as a group, occupied all areas with open formations throughout Africa, as far as there is some vegetation, as well as the warmer parts of the Palaearctic and part of the Oriental Region. The ten species occurring outside the Afrotropics (including SW. Arabia) belong to three species groups. Their distributions are as follows:

phlomidis group. Three species from SE. Europe to C. Asia, one species, viz., *doris*, from Kenya through the Middle East to Pakistan, and isolated in Morocco.

sertorius group. Two species in the Palaearctic, viz., *sertorius* and *orbifer*, forming a superspecies; one species in the Oriental Region, viz., *galba*, forming a superspecies with the fourth member of the species group, *mafa,* which occurs from S. Africa through E. Africa to E. Arabia (Oman).

delagoae group. Six species from S. Africa to Kenya; one of these, *zebra,* in E. Africa and Pakistan, and another, *mangana,* extending from E. Africa into Arabia as far east as Ras Fartak, halfway along the outher coast.

The pattern that emerges from these distribution data shows a contact between the Afrotropics and the areas outside through Arabia and not via West Africa. The Arabian connection is still more obvious, if we consider that three more species (*spio, diomus,* and *colotes*) extend from Africa into SW. Arabia, though without crossing the Arabian desert belt. This pattern agrees well with what is found in other butterflies (De Jong, 1976), but it does not explain why there is no connection between the Afrotropics and the Palaearctic in West Africa. In principle there are two possible explanations for the absence of a West African connection in *Spialia,* viz., (1) *Spialia* species once crossed the Western Sahara, but became extinct in Northwest Africa because of adverse climatic conditions, and (2) *Spialia* species never crossed the Western Sahara. The following arguments are in favour of the latter explanation:

1. In the West African open formations only three *Spialia* species occur, viz., *spio, diomus* and *dromus.* These species also occur in East Africa, where nine more species occur. So if only the number of species is considered, the chance of a West African connection is smaller than that of an Arabian connection.

2. The *Spialia* species that occur in West Africa have a very wide distribution in Africa, indicating that they are not very dainty in the choice of their habitats. Nevertheless, there are no traces of a crossing of the eastern part of the Saharo-Arabian desert belt by these species. If they were not able to traverse the desert belt in the east, where many other species succeeded, why should they have succeeded in the west?

3. There is no differentiation between the populations of *spio, diomus,* and *dromus* in West and East Africa, though there have existed important geographic barriers between West and East African open formations (see below). It means that the species came to West Africa only recently and too late to make use of the opportunities provided by the humid Postglacial Climatic Optimum to cross the Western Sahara, or that they are so eclectic that the barriers mentioned are no real barriers to them. In the latter case, however, we should expect that they made use of the opportunities to cross the Saharo-Arabian desert belt in the east (see also under Speciation patterns).

It may be thought that the occurrence of two other *Spialia* species, viz., *sertorius* and *doris,* in Northwest Africa made it impossible to *spio, diomus* and *dromus* to establish themselves in that area, but as the food plants of *sertorius* and *doris* are quite different from those of the Afrotropical *Spialia* species, this is very improbable.

As said above nine of the twelve *Spialia* species in East Africa, and more precisely in Uganda and Kenya, do not occur northwest of that area. This can only be understood by supposing the existence of an effective barrier between the open formations in East Africa and north of the belt of lowland evergreen forest. It must have been so effective that only three species succeeded in crossing it and so eventually reached West Africa, apparently in a recent time (see above). If we consider that the lowland forest extends as far east as West Uganda, and may have extended to West Kenya in rather recent times, it seems most plausible to look for the barrier in the area between the lowland forest and the Ethiopian highlands, the area that connects the East African plains with the open formations north of the forest belt. Here we find at the present time a very extensive swamp area, the Sudd region (Sudd is an Arabic word meaning "blockage", and relates to the difficult passage for boats), extending west and east of the White Nile in Southern Sudan and covering about 40.000 km^2 of permanent swamp, while about twice that area is flooded by seasonal inundation (Beadle, 1974; Rzóska, 1976). It is through broad water courses and lakes (Lake Albert, Lake Kioga) connected to Lake Victoria and the lowland forest belt. Such an area must be an effective barrier to the drought-loving *Spialia* species. Moreover, at least during the last 40.000 years the level of Lake Turkana (= Lake Rudolf) in North Kenya has changed repeatedly and has been up to 80 m above the present level, causing an overflow to the northwest, to the present Lotigipi Swamp (Livingstone, 1976). This swamp may have drained into the White Nile by way of the present Kenamuke Swamp and Pibor River, thus much extending the barrier to the *Spialia* species at times.

The age of the swampy region is, however, uncertain. According to Livingstone (1976: 27), "the deposits of the existing "Sudd", the Upper Nile Swamps, though presumably dating only from times since the end of the last interpluvial, deserve careful stratigraphic investigation." Moreover, at present a zone of deciduous savanna woodland extends to the southwest of the flood region (Rzóska & Wickens, 1976). Although a more humid period could easily have led to a connection between the lowland forest and the swamps, it is difficult to understand how conditions drier than at present, or even the present condition can have brought about the development of a barrier to expansion to the northwest. So for the time being we must be content with the presumption that the swamps of Southern Sudan, in combination with the Ethiopian highlands, the lowland forest belt, and unknown factors have acted as a barrier to *Spialia* species for such a long time, that the evolution of the genus took mainly place in East and South Africa. It is interesting to note that in the area concerned (i.e. Southern Sudan) overlap occurs of the faunas of the Sudanese and Somali zones (Carcasson, 1964). It implies that the area acted as a barrier to other animals as well, but it does not solve the problem of what exactly formed the barrier.

Speciation patterns

Starting from a speciation sequence as described in Chapter 4, a distinct geographic pattern of speciation arises from the north—south vicariance of sister groups at various taxonomic levels. The following vicariances can be distinguished:

1. at the species group level: *phlomidis* group north of the Saharo—Arabian desert belt (with slight penetration into the Afrotropics by *doris*), *spio* group south of the desert belt;

2. at the species level: *asterodia* + *agylla* in southern Africa, *kituina* in East Africa; *mafa* + *galba* south and east of the Saharo-Arabian desert belt, *sertorius* + *orbifer* north of it; *mafa* in Africa, *galba* in the Orientalis; *wrefordi* in East Africa, its sister group further south (with secondary expansion to the north); *paula* in southern Africa, its sister group further north (with secondary expansion to the south); *mangana* in East Africa and SW. Arabia, its sister group in southern Africa (with secondary expansion to the north); *nanus* in South Africa, *delagoae* further north; *sataspes* in South Africa, *zebra* in East Africa and Pakistan;

3. at the subspecies level: *diomus ferax* in southern Africa, *diomus diomus* further north; *colotes transvaaliae* from South to East Africa, *colotes semiconfluens* in Northeast Africa; *confusa confusa* from southern Africa to Tanzania, *confusa obscura* in N. Tanzania and Kenya; *mafa mafa* from South to Central Africa, *mafa higginsi* in East Africa; *depauperata australis* in southern Africa, *depauperata depauperata* in East Africa.

This pattern suggests a repeated fragmentation of the open formations, and agrees with the current idea of speciation by geographic isolation (allopatric speciation). It is only remarkable that the pattern is still so well discernible, though the isolation of the fragments may have been initiated long ago. However, as long as our knowledge of the exact ecological requirements of the species is so fragmentary, there is little use in speculating on the reasons for particular distributions, and we can only speak in general terms. It is, moreover, plausible that during speciation ecological requirements change in the same way as morphological characters, so that the barrier to range extension can be different before and after the speciation has taken place. Only two kinds of barriers will have been effective for all *Spialia* species (except for the forest species *ploetzi*), viz., desert and dense forest.

The Afrotropical Region

As no past or present east—west extension of desert conditions across the whole African continent south of the Sahara is known, a major factor in the disruption of the distribution of *Spialia* species in the Afrotropics must have been the extension of forests across the continent during wetter and/or colder periods in the Pleistocene (Carcasson, 1964; Moreau, 1966; van Zinderen Bakker, 1967). If only the forest formed the barrier, the subsequent retreat of the forest must have allowed range extensions of the *Spialia* species, obscuring the area of the previous isolation. We can imagine that in this way the following sister group originated: *spio*—*diomus*, *colotes*—*confusa*, and *secessus*—*dromus*, and possibly also *colotes* group—*sertorius* group, all broadly sympatric because the barriers to their distribution are only or mainly dense forest and desert. The restricted range of some other species, however, indicate that not only dense forest, but also some kinds of open formations act as a barrier. At least in East Africa the species concerned are restricted to dry areas (*kituina*, *wrefordi*, *mangana*, and *zebra*), while their sister groups are, or presumably have been, confined to grasslands in southern Africa. If we suppose that the ancestors of these groups of sister species had similar (though probably not identical) ecological requirements, the existence in the past of a corridor of dry savanna from East to South Africa must be presumed. Such a condition can have existed during dry periods. Hamilton (1974) supposed that a connection was possible for the last time 25.000 — 12.000 BP. In view of the further differentiation of the southern sister groups, especially those of *mangana* and *wrefordi,* dry conditions enabling the north—south connection must have also existed much earlier.

It must be noted here that the disjunction concerned shows some resemblance to the well-known Somalia-SW. Africa disjunctions of arid flora and fauna. Indeed, at least two species, viz. *mangana* and *wrefordi,* are confined to the dry thornbush habitat. However, the sister groups of the northern species are not restricted to or do not at all occur in the arid SW. African (Namibia) habitat. Thus, the ancestors of the pairs of sister groups showing north—south vicariance may have become adapted to a richer vegetation than found in the arid Somali zone, with greater possibilities for north—south connections. In that case the present habitat preference of *wrefordi* and *mangana* would be a secondary development. In favour of this idea is also the supposed further development of their respective sister groups. In both cases the sister groups not only differentiated, but also extended northwards, eventually reaching the less differentiated *wrefordi* and *mangana.* Possibly, the northern species could not keep up the competition with the new arrivals and were chased away into less hospitable land.

There are only five *Spialia* species that show subspecific variation in Subsaharan Africa. In three of them, viz., *diomus, mafa,* and *depauperata,* the zone of contact between the northern and southern subspecies is situated somewhere in Zambia-Malawi. This pattern may indicate a common history of the species concerned, which was influenced by the extension of lowland forest to the east and/or the extension of montane biota in East Africa during the late Pleistocene (cf. Moreau, 1966). For *mafa,* however, it is not likely that montane biota acted as a barrier, as this species is well capable of living in the present montane belt in Kenya.

The fact that there is a clear north—south vicariance of subspecies in *diomus* that does not occur in the two other wide-ranging *Spialia* species, *spio* and *dromus,* is a reflection of differences in habitat preference: *diomus* prefers more open and drier conditions than the other species and is for that reason more liable to range fragmentation during humid periods. It is therefore remarkable, that not only *spio* and *dromus,* but also *diomus* do not show subspecific differences between the populations of West and East Africa, though the swampy Sudd region in Southern Sudan must have acted as a barrier during humid periods. Moreover, further west another, probably still more effective, barrier existed during humid periods, viz., a much extended Lake Chad (Megachad), at its greatest extension stretching from the lowland forest to the Tibesti Mountains in the Central Sahara. The last expansion of the lake occurred no longer than 5.400 years ago (Beadle, 1974). The absence of traces of the isolating effect of these barriers in the populations of *diomus* in West and East Africa can only be understood by supposing that *diomus* entered West Africa only after the blockade caused by these barriers was removed.

A special problem is posed by the origin of the forest species *Spialia ploetzi,* as it is difficult to understand the advantage of an adaptation to a completely different habitat, except for reasons of competition. Unfortunately, the problem of change of habitat preference from savanna to forest (and vice versa) has not yet attained attention from the evolutionary point of view, though it must have acted a part in many more lepidopterous genera: of the 63 larger genera of African butterflies listed by Carcasson (1964), 33 have representatives in the forest as well as in open formations. For the time being we must be content with signalizing the problem.

Another point is the subspecific differentiation of *ploetzi.* The boundary between the two subspecies is at or close to the Cameroun—Nigerian border, apparently west of the Cameroun highlands. A similar situation is found in the Satyridae *Bicyclus ignobilis* (Butler) and *B. sanaos* (Hewitson) (Condamin, 1973) and will undoubtedly occur in many other Lepidoptera as well. The origin of this type of differentiation is uncertain and may be complex. The Cameroun highlands, though not acting as a barrier now, may have done so during a colder period, but that does not explain why the highlands are now populated by the eastern form. On the other hand, a dry period would have reduced and fragmented the West African forest area, so that there was no forest left between the River Niger and the Cameroun highlands (see, e.g., Booth, 1958). According to van Zinderen Bakker (1967) a dry, as well as cold period in West Africa was at least partly coeval with the Last Würm Maximum. It is therefore plausible to suppose that the subspecific differentiation of *ploetzi* dates from that time. We shall leave the speculation on the history of this species at that, as it falls outside the scope of the general history of *Spialia.*

The Saharo-Arabian desert zone

The Saharo—Arabian belt of desert has exercised much influence on the history and evolution of *Spialia.* According to Moreau (1952, 1966), the climate of the Suez and Red Sea areas and Arabia seems to have been similar to that of the present day since post-Miocene times, with a somewhat more abundant vegetation during humid periods in mountainous areas. I have not found observations on how far the Nile Valley can have acted as a corridor for north—south exchange since the Miocene, but as the Red Sea area was probably never better than semi-arid, the Nile Valley may never have been more than a relatively narrow corridor of riverine forest with a belt of wooded savanna passing into semidesert with increasing distance from the river. Consequently, during the period we may suppose *Spialia* to have evolved to the present situation, the contact between the African and Eurasian faunas of open formations more humid than semidesert was repeatedly broken and re-established, and there are no indications of a connection over a broad front. A broad front connection existed in the Western Sahara up to about 5.000 years ago, but apparently *Spialia* did not play a part in it (see above).

Leaving the Western Sahara out of consideration, three corridors leading out of and into the Afrotropics were open during humid periods:

1. Nile Valley and mountains west of the Red Sea. For an interesting discussion of climatic and faunistic changes, see Rzóska e.a. (1976).
2. Mountains east of the Red Sea. Higher and more contiguous than the mountains west of the Red Sea. For the relative importance of this corridor, see De Jong (1976).
3. Elevated southern rim of the Arabian Peninsula. According to Moreau (1966) this area may have had a savanna-like vegetation during humid periods. The importance of this corridor is illustrated by the fact that almost half of the species of Rhopalocera occurring in Eastern Oman have an Afrotropical or Indo-Afrotropical distribution (Larsen, 1977). The general lowering of the sea level during the glacial periods must have drained the shallow Persian Gulf, allowing a faunal exchange over land between the Afrotropical and Oriental Regions.

The contact across the eastern part of the Saharo—Arabian desert zone is illustrated by the following pairs of vicarious taxa: *spio* group — *phlomidis* group, superspecies *mafa* — superspecies *sertorius, mafa* — *galba;* and by the occurrence of two species, viz., *zebra* and *doris,* north as well as south of the desert belt. The divergence of the degree of differentiation after severing of the contact, ranging from hardly any differentiation to species group level, suggests that the desert belt was crossed several times, in agreement with what is found in other butterflies (De Jong, 1976).

In view of the present distribution of the relevant taxa, the corridors were equally important. The first two corridors were used by the ancestor of the *sertorius* group, probably by the ancestor of the *spio* + *phlomidis* group, and by *doris* and *mafa,* while the third corridor was not only used by *zebra* and the ancestor of superspecies *mafa,* but to some extent also by *mafa* and *mangana.* It is interesting to note that the present distribution of *doris* and *mafa* clearly shows that these species used the corridors east as well as west of the Red Sea. As *mafa* availed itself also of the opportunity given by the third corridor, it can be called the most expansive *Spialia* species. The ancestors of superspecies *mafa* and of the entire *sertorius* group were apparently also expansive, so that one wonders whether such a trait could be hereditary.

As *mafa* and *mangana* have not completed the crossing of the desert belt, the direction of their expansion is easily detectable: apparently they came from Africa. For the other groups concerned the direction of spread cannot be inferred directly from the present distribution and some reasoning is needed to find plausible solutions, as follows. The sister group of *zebra,* and all successive sister groups when going down along the phylogenetic tree of the *delagoae* group (fig. 119) are African. If we do not conclude from this that the occurrence of *zebra* in Pakistan is due to an invasion from Africa, we are forced to assume that almost all species of the *delagoae* group originated from invasions from the east, successively *mangana, nanus* + *delagoae, depauperata,* and *sataspes,* while a fifth invasion brought *zebra* to Africa. This is less plausible than the assumption of an African origin of *zebra.* Reasoning along the same lines leads us to the conclusion that *doris (phlomidis* group) is a Palaearctic intruder in Africa, while *galba* and superspecies *sertorius* (both *sertorius* group) originate from a northward traverse of the desert belt (or rather from two African intrusions, the first bringing the ancestor of the *sertorius* group to the Palaearctic, where it differentiated into the ancestor of superspecies *sertorius*). For the further geographic and evolutionary history of the *phlomidis* and *sertorius* groups the reader is referred to De Jong (1974).

The last pair of vicarious taxa (*spio* group — *phlomidis* group) can also be supposed to have an African origin, for if the origin was Palaearctic, at least one more crossing of the desert belt would be needed to explain the cleavage of *the spio* + *phlomidis* group and its sister group (fig. 117). Moreover, starting from the assumption that the original food plants of *Spialia* belong to the Malvales (see Chapter 4), the change to Convolvulaceae in the *phlomidis* group, being an adaptation to Palaearctic conditions, would have been reversed in the *spio* group, if the latter originated from a Palaearctic intrusion. This is not a plausible explanation of the present situation. Also when applying the rule of parallelism of chorological and morphological progression, the *phlomidis* group, having more apomorphous characters than the *spio* group, must be considered the chorologically most progressed group. I quite agree with Hennig (1960), that the applicability of this rule is limited, but at least it does not contradict the other arguments.

Humid periods that opened the corridors occurred more than once in the past, for the last time during the Postglacial Climatic Optimum, which ended about 5.000 years ago. From this last opportunity may date the occurrence of *mafa* in Oman. Though mainly living in the highland grasslands in East Africa, the occurrence of *mafa* as far north as Erkowit in Sudan and Ashaira in Saudi-Arabia, and as far east as Oman, where it lives in an Acacia desert landscape, indicates that a relatively small climatic change may enable the species to avail itself of the corridors. For *doris,* which can live in wadi's as far as its food plant (*Convolvulus lanatus*) occurs, a still slighter increase of the humidity was needed to open the corridors. One may even wonder how far the present conditions prevent *doris* from crossing the desert belt.

In view of the differentiation of *galba,* superspecies *sertorius* and the *phlomidis* group, their ancestors must have left Africa during one or more humid periods before the Last Glacial Period. Supposing that speciation in superspecies *sertorius* and the *phlomidis* group took place under the influence of the glaciations in the Western Palaearctic by way of isolations in refugial areas, both taxa must have experienced at least two or three glaciations (see De Jong, 1974). It cannot be stated at the moment whether the three glacial phases of the Last Glacial (Würm) were enough for this development, but together with the two glacial phases of the preceding Riss glacial period (see, e.g., De Lattin, 1967; Moreau, 1955; West, 1968), they certainly were, so that the occurrence of *Spialia* in the Palaearctic does not need to date further back than some 200.000 years.

Contrary to the ancestor of superspecies *sertorius* and probably the ancestor of the *phlomidis* group, the ancestor of *galba* apparently used the eastern route, across the Persian Gulf, as did *zebra*. The best opportunities were provided during glacial periods, when the Persian Gulf was drained. Therefore, the occurrence of these species in India and Pakistan, respectively, is probably not of post-glacial age. The wide distribution and differentiation of *galba* suggests that its ancestor arrived in Asia much earlier than *zebra*, as said above.

6. GENERAL OUTLINE OF THE EVOLUTION OF *SPIALIA*

In Chapters 4 and 5 the phylogeny and geographic history of *Spialia* have been discussed. In the present chapter we shall combine the conclusions into a general outline of the evolution of the genus.

The origin of the genus could not be discussed in the foregoing chapters, as that can only be done by searching for sister groups (according to the method of Hennig, 1966) and, for that reason, needs a comparison with other genera. In advance of a future revision of the genera of the *Pyrgus* group, it may suffice here to state that the ancestor of *Spialia* probably came from the steppes of Central and Western Asia. When and how it arrived in Africa is unknown. Its subsequent development and differentiation took place mainly in Africa. It indicates that there was a rather effective barrier to northward expansions from the very beginning of the genus *Spialia*. Apparently this barrier was the main factor underlying the geographic isolation that led to the origin of the genus. The only possible barrier that comes into consideration is the Saharo-Arabian arid zone. While, however, the main differentiation of *Spialia* took place in the savannas of Eastern and Southern Africa, some other barrier or a combination of barriers must have prevented *Spialia* from occupying the savannas north of the region of the lowland evergreen forest up to a rather recent time. A possible barrier was (and is) the swampy condition of the Upper Nile region (Sudd), but other, unknown, factors must have played a part as well.

The differentiation led in the first place tot the development of three types of male genitalia, especially with regard to the development of the costa of the valva, coinciding with three types of female genitalia, which are, however, less well defined. The three types are represented in the present taxa by the *asterodia* group, the *spio* + *phlomidis* group, and the remainder of the genus, respectively. Each type is distributed at least in Southern and Eastern Africa, obscuring the geographic isolation underlying the origin of the differentiation. The early development of the genus took place in a savanna habitat under not too dry conditions. The present occurrence of some *Spialia* species in dry savanna or semi-desert appears a rather recent development, as undoubtedly is the adaptation of one species (*ploetzi*) to the lowland evergreen forest. The preference for open formations made the ancestors of the present *Spialia* species liable to fragmentation of their ranges by expansion of the forest biota across the African continent. As the occurrence of such expansions can be considered well established and similar expansions of the arid biota are not known, the differentiation of *Spialia* must, in the first place, be attributed to pluvial and/or cold periods that enabled a large-scale extension of the lowland evergreen forest or the montane forest.

The expansions of the forest resulted mainly in the open formations being divided into northern and southern parts. This pattern is still visible in the vicariance of a number of apparent sister groups in *Spialia,* which have been listed in Chapter 5. The fact that the vicariances occur at different taxonomic levels, from subspecies to species group, and the fact that the present distributions of the vicarious groups point to barriers at various places, indicate that the fragmentation of the open formations has occurred repeatedly.

Although periods with large-scale extension of forests are known to have occurred during the Pleistocene, data on the Tertiary climate are very uncertain. The highest number of successive cleavages needed to understand the present differentiation, is eight (viz., in the line leading from the ancestor of *Spialia* to the sister groups *zebra* and *sataspes*). It implies that the development of *Spialia* may mainly, if not entirely, have taken place in the Pleistocene and there is certainly no reason to look for the origin of *Spialia* in a period prior to the Pliocene.

The barriers that kept *Spialia* in Eastern and Southern Africa remained rather effective. The correctness of the assumption, that the arid condition of the Saharo-Arabian desert belt was a main factor inhibiting northward range extension, is indicated by the fact that only species capable of living under dry conditions succeeded in escaping the boundaries of the Afrotropics. Opportunities for such escapes were provided several times during the Pleistocene by increased humidity, for the last time only 7.000—5.000 BP (Postglacial Climatic Optimum). With regard to the opportunities there is no reason to suppose that the occurrence of *Spialia* species outside the Afrotropics dates back from a time prior to the Pleistocene.

The northward expansions took place after the initial three types had differentiated into the ancestors of the present species groups (the differentiation took mainly place in one of the types), a further reason to suppose that only in rather recent times, i.e. in Late Pleistocene, the Palaearctic and Oriental Regions were invaded. If there were earlier invasions, they have left no traces. For an explanation of the differentiation outside Africa it is not necessary to assume that the relevant invasions occurred earlier than the last or at most the one-but-last interglacial period, as the climatic changes since then were sufficient to be responsible for the development of the present differentiation. Consequently there are three kinds of evidence for a geologically spoken, recent occurrence of *Spialia* outside Africa, viz., (1) the advanced state of the differentiation in Africa, (2) the opportunities given, and (3) the differentiation outside Africa.

It is remarkable that the establishment of *Spialia* in the Palaearctic was accompanied by a change of food plants, from Malvaceae or related families to Rosaceae and Convolvulaceae. This may be due to competition. The Malvaceae are supposed to be the original food plants of the *Pyrgus* group. As the ancestor of *Spialia* most probably came from the Palaearctic, a return to the Palaearctic can be supposed to have caused competition, unless the food plants were changed. In this connection the common and wide-spread Palaearctic *Carcharodus alceae* (Esper), a multivoltine species of the *Pyrgus* group and living on various Malvaceae, comes in mind, but we shall not speculate here further on this subject, leaving it for a future discussion on the history of the *Pyrgus* group. Only one more remark about food plants. The faunal exchange between Africa and the areas outside was largely unidirectional as far as *Spialia* is concerned, viz., out of Africa. Only one successful re-invasion of Africa took place, viz., of *doris*. The success of the establishment of *doris* in Africa south of the desert belt may be due, apart from its preference for dry conditions, to the food plant (*Convolvulus*) being entirely different from the food plants of African *Spialia* species.

The connection between Africa and the areas outside was established only by way of the Nile Valley, the Red Sea area and the southern rim of the Arabian Peninsula. This is the more remarkable as the eastern part of the Saharo-Arabian desert belt is supposed to have been always drier than the western part, which was covered by a mediterranean type of vegetation only 7.000—5.000 years BP. The absence of a western connection is probably due to the late arrival of *Spialia* in the West African savannas, as indicated by the absence of differentiation between the populations in East and West Africa of the three species (*spio, diomus,* and *dromus*) that occur in West Africa, while one of these species (*diomus)* does show subspecific variation in Subsaharan Africa, and by the number of cleavages of the evolutionary line since the beginning of the genus, needed for *dromus* (seven), showing that this species itself is young and thus its occurrence in West Africa cannot be old. The main factor that kept *Spialia* so long out of West Africa, probably was the swampy condition of the Upper Nile region, connecting the lowland evergreen forest and the Ethiopian highlands, but other, unknown factors must also have played a part.

7. LITERATURE

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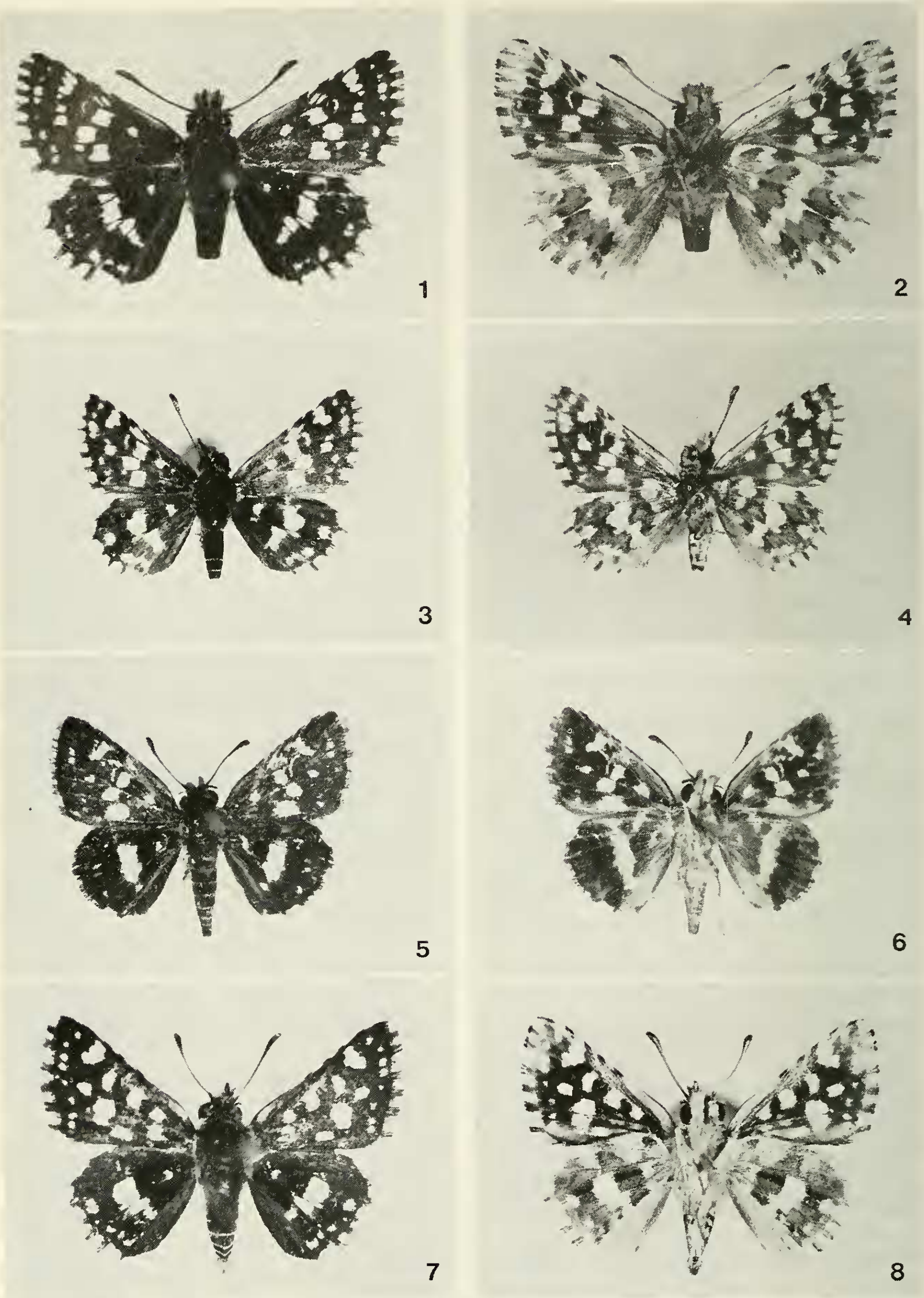
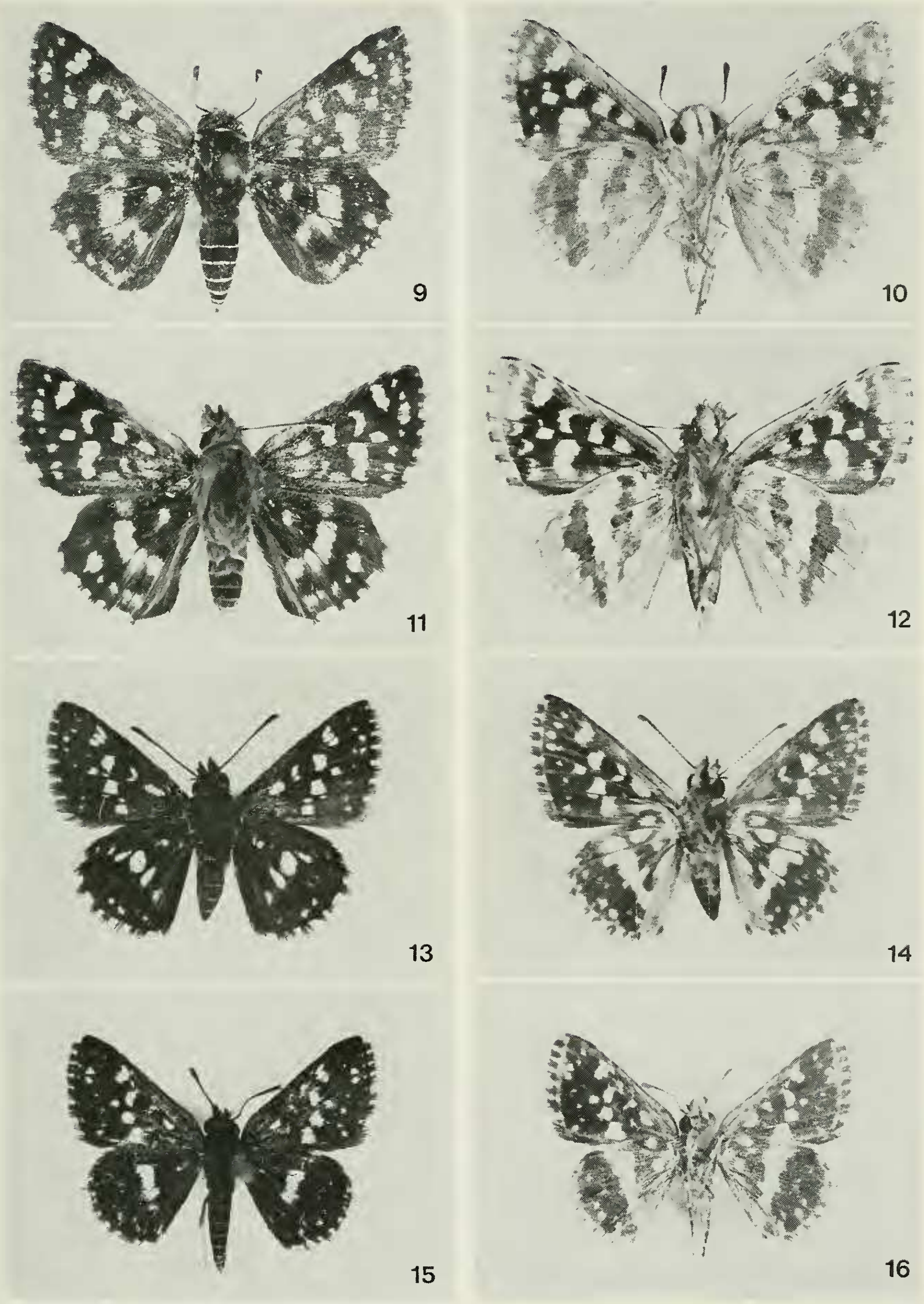


Plate 1.

Figs. 1—8. Upper (left) and underside (right) of *Spialia* species. 1—2, *S. asterodia* (Natal). 3—4, *S. agylla* (Bloemfontein, S. Africa). 5—6, *S. kituina* (Ukunda, Kenya). 7—8, *S. spio* (Naro Moru, Kenya).



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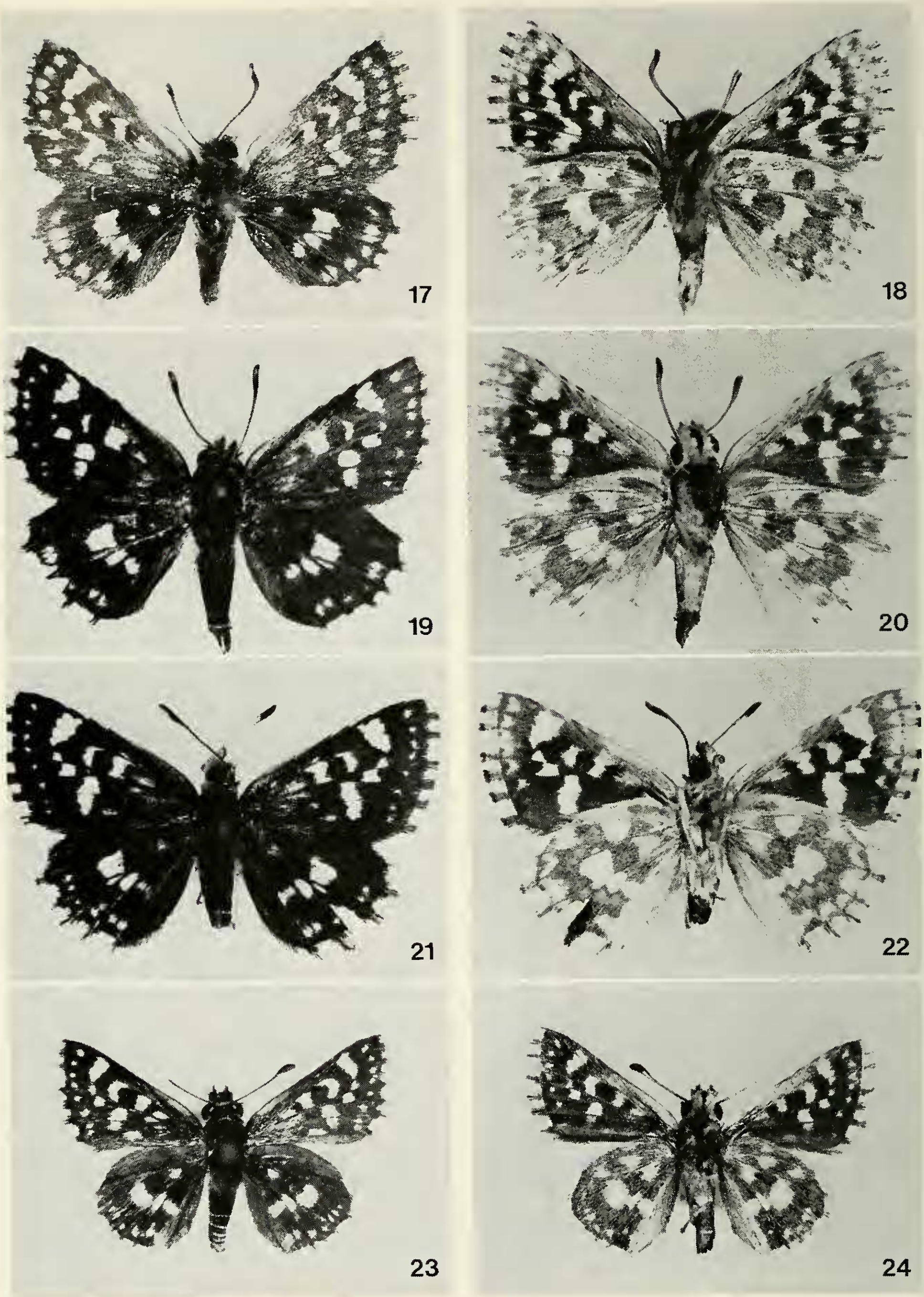
Figs. 9—16. Upper (left) and underside (right) of *Spialia* species. 9—10, *S. diomus diomus* (Ukunda, Kenya). 11—12, *S. diomus ferax* (Sheldon, S. Africa). 13—14, *S. colotes semiconfluens* (Bihendula, Somalia). 15—16, *S. confusa obscura* (Arabuko Forest, Kenya).



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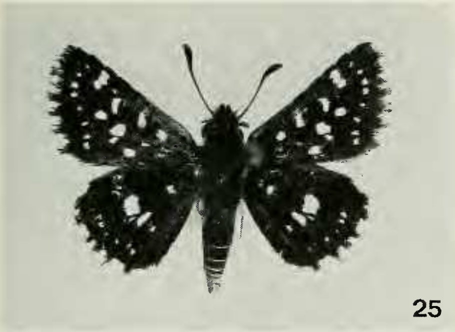
Figs. 17—24. Upper (left) and underside (right) of *Spialia* species. 17—18, *S. phlomidis hermona* (Mt. Hermon). 19—20, *S. osthelderi gecko* (Kopet Dagh, Turkmenia). 21—22, *S. geron struvei* (Kotgai, E. Afghanistan). 23—24, *S. doris evanida* (Karachi, Pakistan).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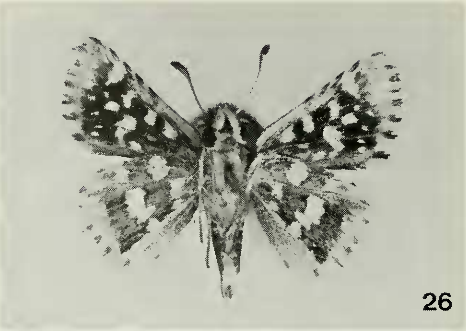
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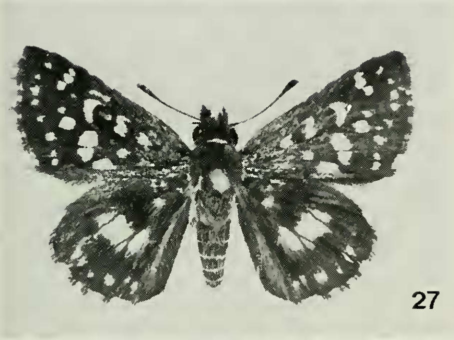
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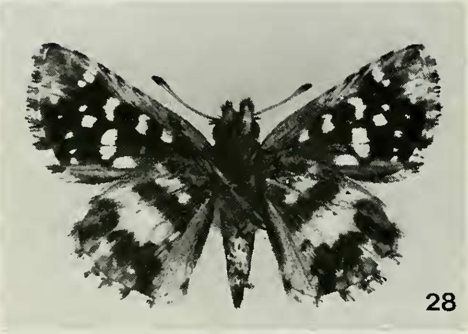
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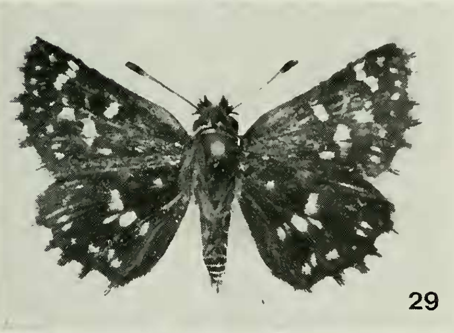
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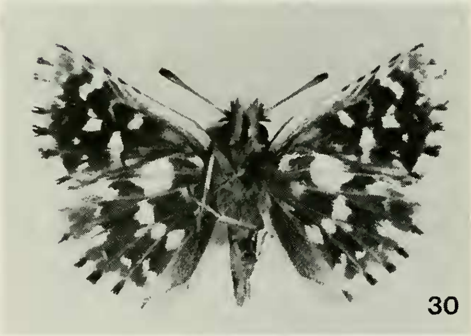
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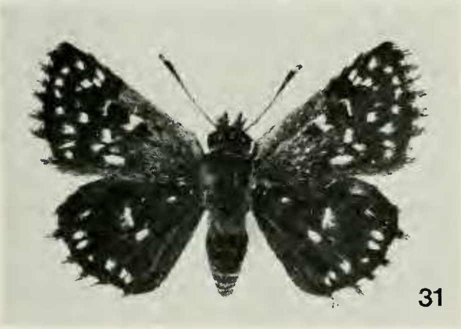
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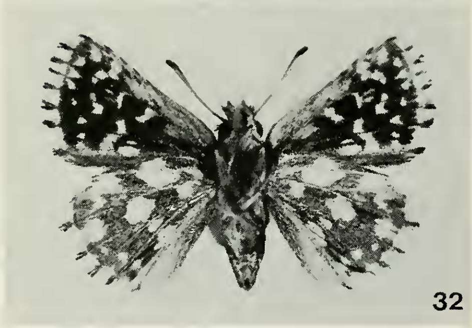
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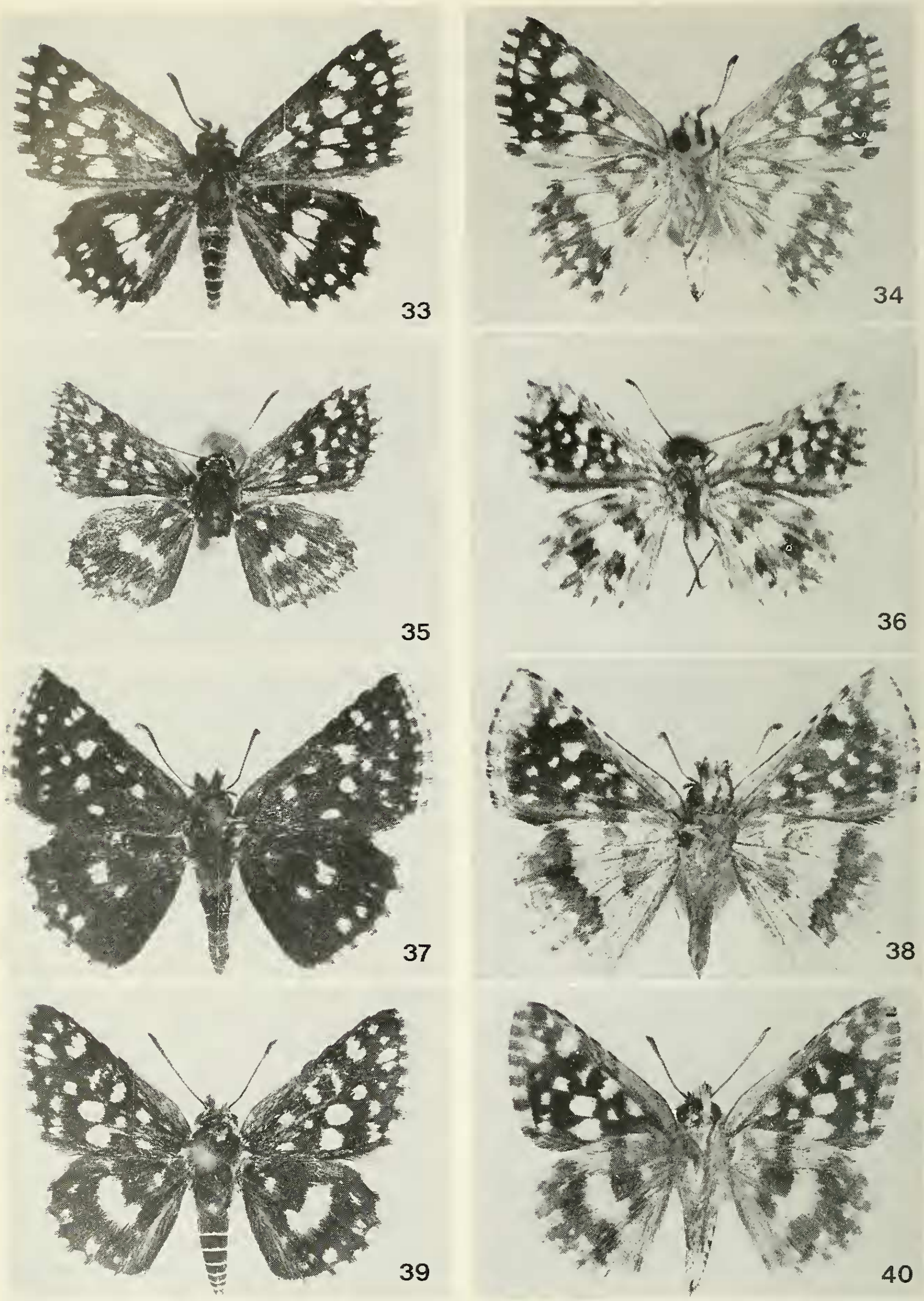
Plate 4.

Figs. 25—32. Upper (left) and underside (right) of *Spialia* species. 25—26, *S. mafa higginsi* (Naro Moru, Kenya). 27—28, *S. galba galba* (Haldumulla, Ceylon). 29—30, *S. sertorius sertorius* (Switzerland). 31—32, *S. orbifer orbifer* (Sarajevo, Jugoslavia).



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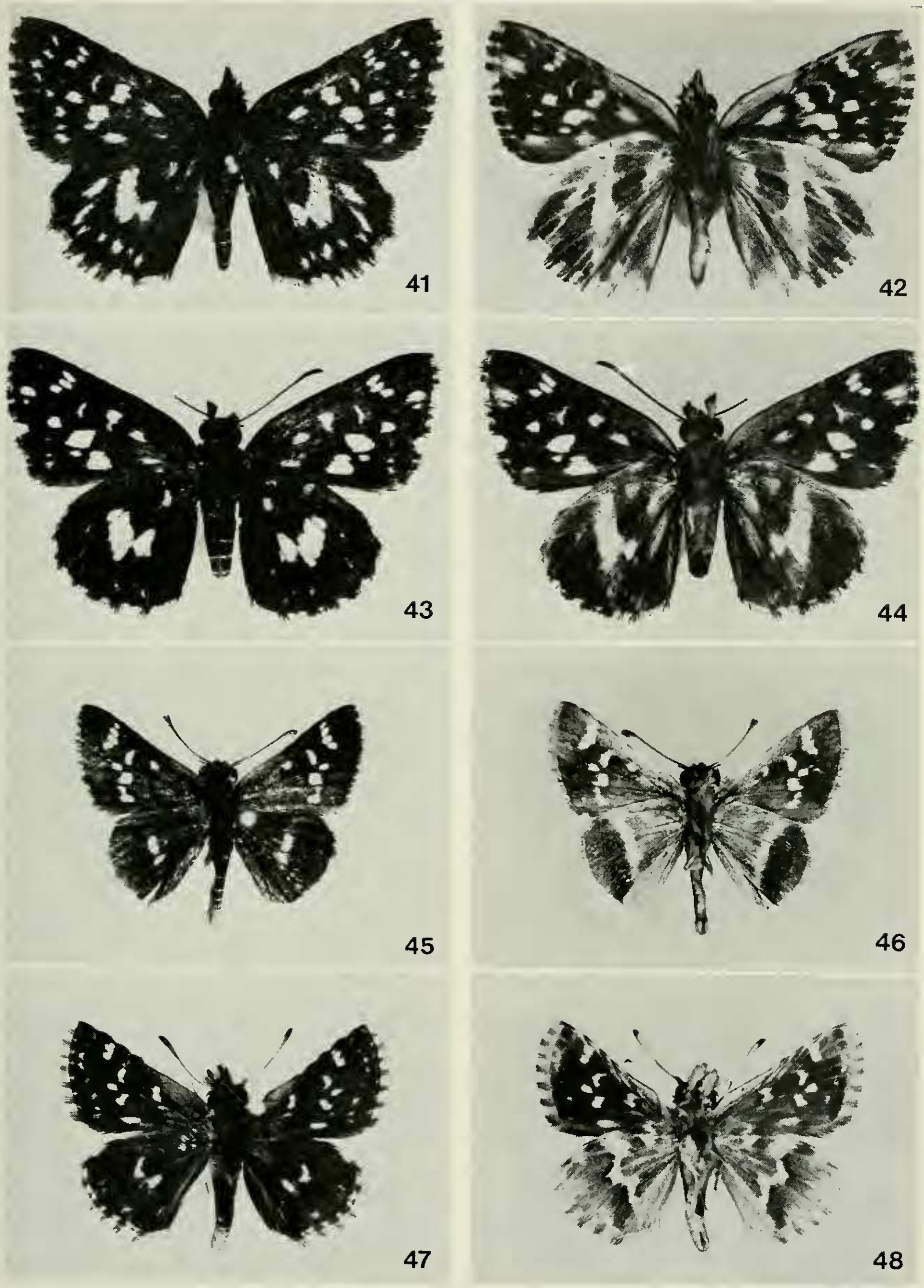
Figs. 33—40. Upper (left) and underside (right) of *Spialia* species. 33—34, *S. wrefordi* (Samburu N. P., Kenya). 35—36, *S. paula* (Essexvale, Rhodesia). 37—38, *S. secessus* f. *trimeni* (Mpanda, Tanzania). 39—40, *S. dromus* (Mpanda, Tanzania).



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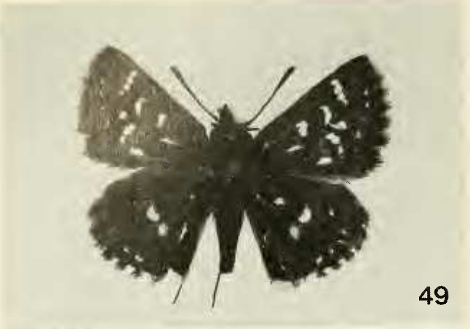
Figs. 41—48. Upper (left) and underside (right) of *Spialia* species. 41—42, *S. ploetzi ploetzi* (Bitje, Cameroun). 43—44, *S. ploetzi occidentalis* (Warri, Nigeria). 45—46, *S. mangana* (Dire Daoua, Ethiopia). 47—48, *S. nanus* (Sheldon, S. Africa).



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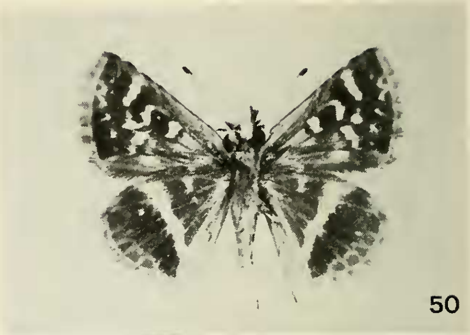

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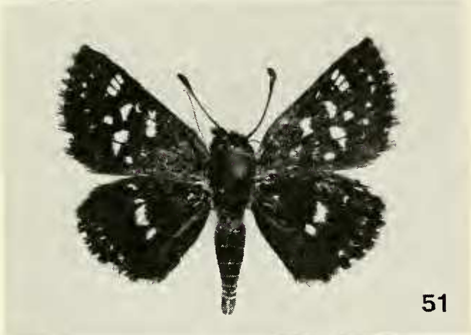

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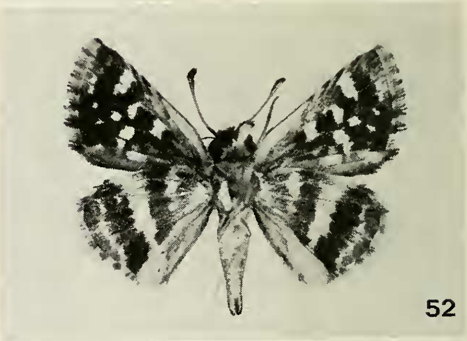

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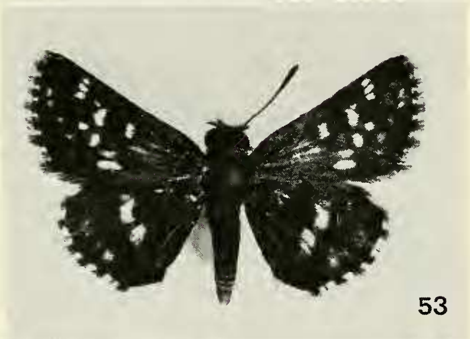

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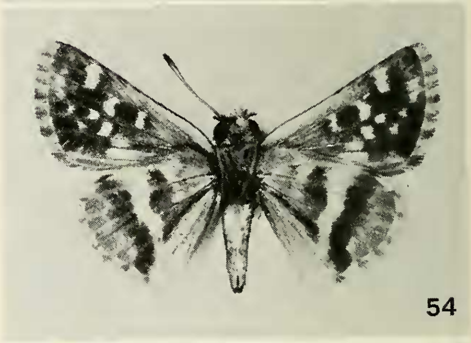

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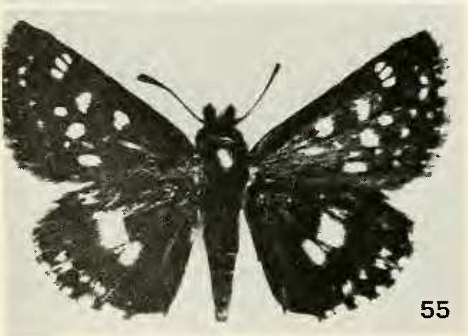

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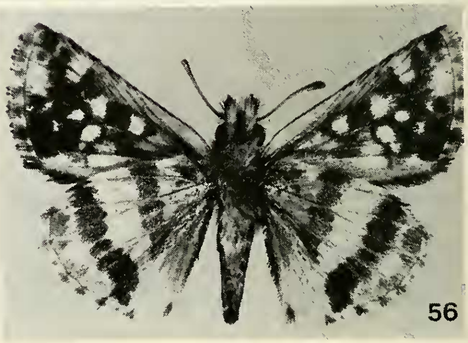

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Plate 7.
Figs. 49—56. Upper (left) and underside (right) of *Spialia* species. 49—50, *S. delagoae* (Muden, Natal). 51—52, *S. zebra bifida* (Ukunda, Kenya). 53—54, *S. sataspes* (King Williamstown, S. Africa). 55—56, *S. depauperata depauperata* (Mlanje, Malawi).